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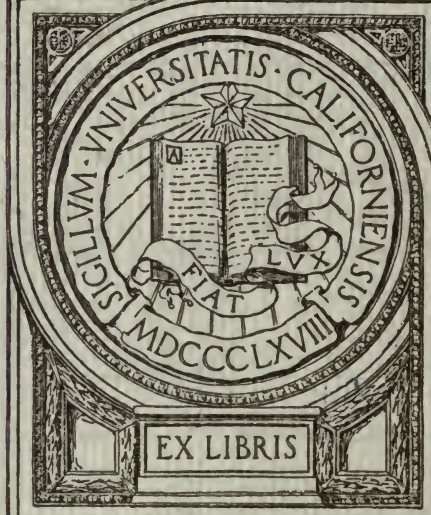


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# SCIENTIFIC BOTANY;

OR,

## BOTANY AS AN INDUCTIVE SCIENCE.

BY

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# TRANSLATOR'S PREFACE.

In producing this work of Professor Schleiden in an English dress, I feel that the reputation of the Author and the Work alike render any apology unnecessary; but I am conscious that I owe some explanation to the Public, both as to the manner of the translation and the delay in its appearance.

The second German edition of this Work, of which the present volume is a translation, was accompanied with a Methodological Introduction, intended as a development of those general principles of science, which are derived from a study of the observing mind, and the observed external nature. As the discussion of these general principles occupies a considerable space in the original, and it was deemed desirable not to increase the bulk of the present Work, this Introduction has been omitted. In its place I have, however, inserted a short summary of these observations, as they have been given by the Author himself in his "Grundriss der Botanik," which work consists of the text of the present volume without the explanatory comments. This summary is given in the four first paragraphs of the present translation.* In the original Introduction a considerable portion is occupied with the description of the microscope, and its application to scientific researches; as the observations of the Author seem to me to be judicious, and we have none of precisely the same kind in our own language, and especially as this book may fall into the hands of students who are not acquainted with the powers or the manner of using this instrument, I have thought it right to reproduce this portion of the Introduction.†

With the exception of those parts of the Introduction referred to, and in not more than two or three instances, of matters in the notes that were not deemed relevant to the translation, nothing has been omitted in the present Work.

* As general introductions on the principles involved in scientific inquiry, we have in our own language two admirable works,—Sir John Herschell's "Discourse on the Study of Natural Philosophy," and Professor Whewell's "Philosophy of the Inductive Sciences."

† Appendix D.

I feel that some portions of the Translation are open to the charge of inelegance, and this has arisen from my anxiety rather to give a correct notion of the Author's meaning than, by the use of other language, to diminish the force of the original.

The delay in the publication has been owing in part to ill-health, and in part to the pressure of other engagements. I have only now been enabled to produce it thus early in the year through the kind assistance of my friend, Mr. Arthur Henfrey, who has not only revised the whole of the Morphology, but translated several sheets. I am also indebted to Mr. Henfrey for the translation of the new matter in the third German edition of the Work, which will be found in the Appendix. I have likewise to offer my thanks to my friends, Dr. Day and Mr. Busk, for much valuable assistance; and to another friend, for kindly revising the proof-sheets of the whole Work.

22. Old Burlington Street, London,
April, 1849.

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# PRINCIPLES

OF

# SCIENTIFIC BOTANY.

## INTRODUCTION.

BOTANY, as an inductive science, comprehends the study of the laws and forms of the Vegetable Kingdom. As an experimental science, it takes a very low position; and, at present, embraces but a very narrow circle of actually established facts, few indications of natural laws, and no fundamental principles and ideas by which it might be developed. This becomes very obvious when even the answer to the question, "What is a Plant?" is yet a problem of Botany. Hence, it must proceed with its researches upon undoubted plants, and extend itself cautiously and exclusively in the path of Induction.

§ 1. Botany is a branch of the one and entire Science of Nature: since this embraces the laws of Physics and Chemistry, these are indispensable branches of preliminary knowledge. Botany is also, in itself, Science; consequently the highest product of the activity of the human understanding: but this may be led into error, and follow wrong paths. If we would find truth, we must know accurately what are the laws according to which the powers of the mind work. Botany, therefere, requires a philosophical culture, that is, knowledge of a theory of the intelligent Reason, founded upon an empirical Psychology; in a word, a critical Philosophy.

§ 2. The objects of Botany are actual existences — natural bodies. These must be examined in all possible ways; and to this many aids are necessary, for even the parts invisible to the naked eye must be investigated.

Those who wish to make solid advances in the science of Botany will find the following instruments indispensably necessary: —

1. A microscope.*
2. A good pocket lens.
2. Scissors, knife, needle, and pincers.
4. Certain re-agents, — as Iodine dissolved separately in water and in alcohol, liquid Ammonia, Sulphuric Acid, Nitric Acid, Alcohol, Ether, &c.

§ 3. In relation to other sciences, Botany has to solve the following problems: —

1. For Chemistry, must be resolved in the plant, as in the simplest case, the question how organic combinations arise from inorganic elements.
2. For Physiology to lay its simplest and most general foundations.

Hence it is an indispensable branch of knowledge for the Chemist and the Physiologist.

In practical applications it subserves:

1. Agriculture; as it teaches the conditions of the life of plants.
2. Pharmacy; as it affords a knowledge of the officinal plants, and gives, through the study of structural relations, the most secure and often the only indications for the distinction of the drugs derived from the vegetable kingdom.

In all these cases, it is the physiology of plants which is alone of use. A knowledge of the systematic arrangement of plants is only of importance to the botanist: for all others it is a pastime, if not a waste of time.

§ 4. The facts of the whole science, for the sake of study and facility of comprehension, may be divided in the most intelligible manner according to the following scheme: —

1. Vegetable Chemistry.
2. Study of the Plant-Cell.
3. Morphology, or study of the Forms of Plants and their Organs.
4. Organology, or study of the Life of the entire Plant and its Organs.

* See Preface.

# FIRST BOOK.

# CHEMISTRY OF PLANTS.

---

## CHAPTER I.

### THE INORGANIC ELEMENTS.

§ 5. THE elementary bodies found in plants are the following: — 1. Carbon (C); 2. Hydrogen (H); 3. Oxygen (O); 4. Nitrogen (N); 5. Chlorine (Cl); 6. Iodine (I); 7. Bromine (Br); 8. Sulphur (S); 9. Phosphorus (P); 10. Silicium (Si); 11. Potassium (K); 12. Sodium (Na); 13. Calcium (Ca); 14. Magnesium (Mg); 15. Aluminium (Al); 16. Iron (Fe); 17. Manganese (Ma); 18. Copper (Cu).

These substances occur in very varying proportions in plants. Carbon is of all the most important and the most abundant. It forms the skeleton, the solid basis, of all plants. By careful charring, the minutest parts of the texture of plants may be preserved, and almost everything is consumed or driven off except the Carbon. In the spontaneous decomposition of plants, it also remains longest unchanged; and the entire structure of the plant is often retained in peat and coal, so that the families and genera of the plants can be recognised. Carbon is never found pure in plants.

Hydrogen and Oxygen form, with Carbon, most of the proximate principles of plants, and in the more important substances they occur in the proportion in which they form water. Oxygen is found free in plants dissolved in their juices. Hydrogen is also found free in the Fungi.

Nitrogen in combination with the foregoing elements form some of the most important secretions of plants. Whether it is found free in the Fungi, is not yet well made out.

Chlorine, Iodine, and Bromine, are found in the form of salts. The first in plants of the sea-shore; the two last in those growing in the sea.

Sulphur and Phosphorus are found in most plants as sulphuric and phosphoric acids (the last is especially abundant in the membranes of the seed in grasses). They both enter into combination with protein to form albumen, casein, &c.

Silicium is present in all plants as silica; often in very large quantities, as is shown by the following analysis of the ashes of several plants: —

The ashes of *Equisetum limosum* yielded 94·85 per cent of silica
*Equisetum arvense* . . 95.48 „
*Equisetum hyemale* . . 97·52 „
*Calamus Rotang* . . 97·20* „

Where the silica is in very large quantities, as in the bark and epidermis of the larger grasses, the tubular palms, and the equisetums, the ashes by careful burning may be made to retain the form of the plant so accurately, that even microscopic organs may be readily distinguished.† The silica in these plants exists in the form of small plates, grains, or needles, which are often melted together by the heat; but if the part of the plant is submitted to the action of sulphuric acid, the silica retains its primitive forms. This proves that the silicium is not chemically united with the tissue of the plant, as is stated by Reade‡; or even, indeed, organised, as was formerly gratuitously maintained.

Potassium, Sodium, Calcium, Magnesium, Aluminium, Iron, Manganese, and Copper, are present only as oxides in combination with acids. The first seven exist in very varying proportions in most plants: copper probably in only a few. There is an old saying among the people, especially in the north of Germany, that the wood of the lime contains gold.§

On the origin of these substances in plants, and more particularly with regard to the question as to whether plants take them up from the earth, or form them by a peculiar process of vegetation out of the first four elements above-named, there is but one opinion amongst chemists and physiologists, and that is, that no elementary body can be present in plants that has not been taken up from without the plant. The opposite view, maintained by Reade‖, can only be regarded at the present day as a curiosity, and scarcely deserves reference but for the refutation supplied by the labours of Saussure, Davy, Lassaigne, John, Jablonsky¶, and others. It is difficult also to divine what could have induced the Berlin Academy to give its prize to the single rough experiment made by Schrader, and the confused reasoning of Neumann; which, supported, indeed, by Braconnot, first brought this absurd view into vogue.** If we consider how small the quantity of solid matter is in most plants, and the large quantity of water they take up and allow to evaporate, we shall have no difficulty in accounting for the presence of substances in plants, which, when diffused through the water absorbed, would resist the test of the most delicate re-agents.

§ 6. The foregoing elements form amongst themselves certain binary combinations, of which the following are the most important that are met with in plants:—

*a. Compounds with Oxygen.*—Of these, water (HO or $\dot{H}$) and carbonic acid come first ($CO^2$ or $\ddot{C}$); then oxalic acid ($\overline{O}$ or $C_2O_3$) and the other oxygen acids; and lastly, the oxides of the metals.

Water is the most important: without it no chemical change could take place, to say nothing of vital processes. Most plants contain large

* H. A. Struve de Silica in Plantis nonnulla. Diss. inaug. Berol. 1835. † Ibid.
‡ London and Edinburgh Phil. Mag. and Journ. 1837. Nov.
§ See A. v. Humboldt Floræ Fribergensis Specimen, Berol. 1793, p. 134.
‖ Op. cit.
¶ Jablonsky de Conditionibus Vegetationi necessariis quædam. Diss. inaug. Berol. 1832.
** Ibid. p 78.

quantities of water in their tissues. In one hundred parts of *Ceratophyllum demersum* ninety were found to be water, and ten solid matter.

Carbonic acid is also widely diffused with water: it forms the principal source of nourishment for plants. It is found dissolved in the sap of plants: at night, in almost every plant; in the day, in ripe fruits, in aerial roots, &c. In consequence of the processes of respiration and combustion on the earth, and volcanic agency, the atmosphere contains an inexhaustible supply of carbonic acid for plants.

Oxalic acid is constantly produced by the decomposition of the foregoing compounds, and is found apparently in all plants. It is found free in most succulent plants, as the *Crassulaceæ, Ficoideæ, Cactaceæ**, &c.; also in the hair-glands of *Cicer arietinum.*

*b. Compounds with Hydrogen.*—These are principally ammonia ($NH^3$), hydrochloric, hydriodic, and hydrobromic acids.

Ammonia is probably the source of nitrogen in all plants. It occurs free in the unassimilated sap, as in the spring sap of the birch and the grape vine, and perhaps also in the tissues of unnaturally succulent cultivated plants, as the beet.

§ 7. The foregoing oxides and acids unite together to form salts, some of which are found dissolved in the sap of plants, and others in the form of crystals. The most important are the alkalies in combination with the vegetable acids, or chlorine, bromine, and iodine; then, perhaps, those with sulphuric and phosphoric acids; whether any exist with carbonic acid, is doubtful: next come the earths, with vegetable acids, especially oxalic acid, then with sulphuric and phosphoric acids; and, lastly, the metals mostly in combinations not yet determined. The greater part of the salts are found in the living, vegetating, green parts of plants, as the leaves, &c.; the least, in the wood (Saussure). A certain quantity of these salts appears essential to the life of plants. Ammoniacal salts from the atmosphere appear to be the source of the nitrogen in plants.

Fourcroy and Vauquelin†, long ago, proved that the greater part of the carbonates found in the ashes of plants were formed, during the burning, from other salts of vegetable acids. They proved that almost all plants contain—1. acetate and malate of lime dissolved in the sap; 2. citrate and tartrate of lime, which either exist as a super salt or in a solid form; 3. oxalate of lime in a solid form. All these are found in the ashes of plants as carbonates; but these latter are not to be found if, before the burning, the plants are by turns treated with cold and boiling water and diluted muriatic acid.

The salts of the alkalies are found dissolved in plants, but the insoluble earthy salts present themselves in a crystallised form in the cells. Of these, the oxalate of lime has been most accurately inves-

* Liebig (Annal. xlvi. p. 77.) says the *Cactaceæ* contain tartaric acid; but he is certainly wrong with regard to most *Cactaceæ.*

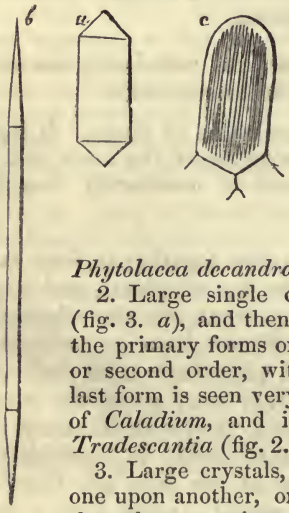
† De la Métherie, Journ. de Physique et de Chim., tome lxviii. p. 429. (1809).

1.

2.

tigated. It appears to be present in every plant, and in some in very large quantities. A stem of *Cereus senilis*, after the water was driven off, contained eight hundred and fifty-five parts oxalate of lime in the thousand. The form of the crystal of oxalate of lime is the quadratic octaedron (fig. 1.); and it presents, like almost all compounds of the earths, as its primary form, the right-angled four-sided prism (in the binaxial and unaxial systems). The following forms are easily distinguished:*—1. Needle-formed crystals (Raphides, *De Cand.*), being a combination of a very long prism with an octaedron (fig. 3. *b*), whose surface, as in the Zircon and the Hyacinth, is united with the surface of the prism. These lie together in bundles of from twenty to thirty in a single cell, which they entirely fill up; and are present in almost all plants, and may be well seen in *Phytolacca decandra* (fig. 3. *c*).

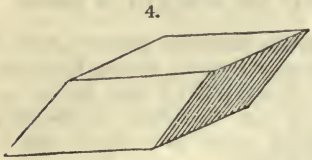
3.




2. Large single crystals, either of the form of the last (fig. 3. *a*), and then very long, as in the *Agave americana*, or the primary forms or combinations, are octaedrons of the first or second order, with two or three blunt or pointed. This last form is seen very beautifully in the pollen of many species of *Caladium*, and in the parenchyma of the old stems of *Tradescantia* (fig. 2.).

3. Large crystals, in which the crystals have developed one upon another, or grown to organic cells in such a way that they constitute irregular-formed glands. They are so common amongst phanerogamous plants at one season of the year or another, that it would be difficult to give an example of a plant in which they do not exist. They are easily observed in the *Cactaceæ*.

4.



Next to oxalic acid with lime, carbonic acid is most frequently found, and this in combination with lime. The carbonate of lime assumes a variety of forms, but most commonly that of the pure rhomboedron (fig. 4.); as, for instance, in the *Cycadaceæ*, in many *Cactaceæ*, and in the leaves of species of *Costus*.

Sulphate of lime is also found, in the form of single or double octaedrons, or in a tabular form, as octaedrons above and below, with

* Even through artificial precipitation, oxalate of lime is never amorphous, but is constantly crystallised, as shown by Valentin, Repertorium, vol. ii. p. 30.

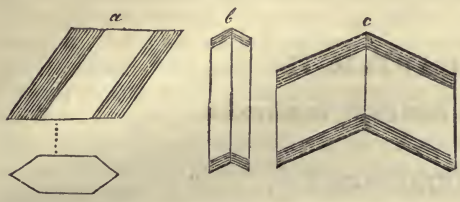
[2] Oxalate of lime as a quadratic octaedron, and a combination of three octaedrons, found in the pollen of a species of *Caladium*.

[3] *a*, Quadratic pillars combined with octaedrons. *b*, The same elongated. *c*, A bundle in a cell.

[4] Carbonate of lime, as seen in the epidermis of *Cactaceæ*.

the end of the prism cut off (fig. 5. *a*); or, what is especially characteristic, in a twin form, like the gypsum crystals of Montmartre. This last form is found in the *Musaceæ* and many *Scitamineæ*.

5.




Such crystals present themselves in all phanerogamous plants, but are not so frequently found in cryptogamic plants. They have been described amongst the latter in *Chætophora*, *Hydrurus*, and *Chara*, where they exist not in the cells but in the intercellular spaces. In *Polysperma* and *Spirogyra* they are found in the cells. In the *Phanerogamia* they lie constantly enclosed in the cells (also in the glands of the air-passages of *Myriophyllum**); more formless crystalline masses, especially of carbonate of lime, are found in the intercellular passages, and upon the leaves of *Lathræa;* and in many species of *Saxifraga*, as *S. Aizoon* and *S. longifolia*, they are seen on the edges of the leaves as true excretions.

*History.*—The discovery of crystals in plants is due to Malpighi, who first figured the glands of *Opuntia* (Anatome Plant. tab. xx. fig. 105. E.). The needle-like crystals were discovered by Jurine (Journ. de Physique, 56.). Meyen and Unger have described various other forms. Buchner was the first to give a chemical analysis, and thought he had found phosphate of lime in them. Raspail showed that they were principally composed of oxalate of lime, which had been previously discovered by Scheele in the roots of rhubarb, but forgotten. Liebig first pointed out that the vegetable acids, in all species of plants, exist combined with a determinate quantity of the base, however different the base may be, and that this quantity depended on the amount of oxygen combined with the base, the oxygen being always in the same proportion in the same species.† The salts of ammonia were first pointed out by Saussure as the source of nitrogen in plants, and afterwards further elucidated by Liebig.‡

* Meyen (Physiologie, vol. i. p. 241.) appears to have overlooked the fine membrane which encloses these glands.

† Liebig, Chemistry in its Applications to Agriculture and Physiology.

‡ Op. cit.

[5] Sulphate of lime: *a*, simple crystal; *b* and *c*, twin crystals. From the petioles of *Musa* and *Strelitzia*.

# CHAPTER II.

## ON THE ORGANIC ELEMENTS.

## SECTION I.

### OF THE ASSIMILATED BODIES.

§ 8. THE four elementary bodies*, Carbon, Oxygen, Hydrogen, and Nitrogen, are associated together as organic or vegetable elements, but they have evidently different values for the life of the plant even in its simplest forms. Next to these we find a series of bodies, which are necessary for the origin and development of cells, and these I call especial assimilated matters.

§ 9. Some of these are substances of which the cell-membrane is formed, or which necessarily precede the formation of it, and which contain only Carbon, Hydrogen, and Oxygen. I shall mention here: 1. Cellulose, or Sclerogen; 2. Amyloid; 3. Vegetable Jelly; 4. Starch; 5. Gum; 6. Sugar; 7. Inulin; 8. Oil of Fat.

1. Cellulose (Sclerogen, Lignine, woody fibre) is completely formed, rather tender, flexible, and elastic, perfectly clear and transparent, and entirely insoluble in all known menstrua. When treated with caustic potash or concentrated sulphuric acid, starch is formed. Like all organic substance it is distended by moisture and contracted by drying. It is permeable to all fluids and actual solutions, which, under some circumstances, are taken in on one side and passed out on the other. Its composition, when analysed, gave the following results:—

| | C | H | O |
|---|---|---|---|
| From the wood of the willow and the beech, according to Prout - - - | 12 | 8 | 8 |
| | 12 | 11 | 11 |
| Various cell-membranes, according to Payen (*Ann. des Sc. Nat.* 1839) - - | 12 | 10 | 10 |

These analyses differ only in the quantity of water they contain.

To me it appears most correct to use the above formula, in which the carbon is reckoned at 12. Mulder, however, takes C 24, H 21, O 21, as isomeric with soluble inulin. Crookewitt has pointed out that this does

* Vier Elemente
Innig gesellt
Bilden das Leben,
Bauen die Welt.

Four elements
Intimately mixed
Give form to life,
Build up the world.

The genius of the poet has here evidently anticipated later chemical discoveries.

not make it a simple substance. Combinations of Cellulose with other bodies are not yet known; there thus remains, to explain the easy transition of Cellulose into Sugar, Dextrin, and Starch, only the hypothesis of Isomerism. All other formulæ appear purely arbitrary, and explain nothing, for the elementary analyses vary from 43·22 to 52·01 of carbon, 5·9 to 6·91 hydrogen, 41·57 to 50·38 oxygen, or of analyses of the same cellular tissue taken into account C 43·2—44·7, H 6·0—6·5, O 49·3—50·59, which agree perfectly with the formula given above. On the other hand, the whole doctrine of an incrusting matter (Payen), although supported by the profundity of Mulder (Physiol. Chem. Moleschott, p. 209.), is a mere castle in the air, that must be rejected *à priori.* On the application of the ordinary re-agents, the thickness of the cell-walls is not diminished, but they become loosened and swell up. What the reagents take up are the contents of the cell, and matters which the cell-wall contain, and which, according to the age of the cell, would become colouring matter, tannin, humic acid, and humates. The wood-cells are, in comparison with other cells, decaying, and are constantly forming out of the cellulose substances, which are more and more rich in carbon, which remain dissolved in the cell-walls, and which are taken up by means of re-agents. The successive layers of the cell-wall are composed chemically out of the same or an isomeric matter as the primary cell, which explains its whole deportment, and even Payen's elementary analysis of the spiral fibres in *Musa sapientum.* A knowledge of the cell-layers is especially important physiologically; a knowledge of the substances which convert sap-wood into heart-wood is only technical, as here life is almost wholly extinct.

Cellulose presents itself under many modifications. In its pure state it appears to vary chemically, according to the quantity of water it contains. Independently of this, it varies greatly in its physical properties, such as brittleness, viscosity, density, and especially in its perviousness to water, which the less it is the more it appears to approach in its nature amyloid and jelly; and there are, in fact, very many transitionary bodies between these three.*

In the impure state in which it ordinarily occurs, it varies yet more from the passage through it of other matters; perhaps through some decomposition which they induce. Its colour is especially various, passing from perfect transparency to the darkest brown (as in ferns); and occasionally all other possible colours are present, as is seen in the epidermis of the seeds of *Leguminosæ*, a golden yellow colour in the leaves of *Phormium tenax*, &c.

2. *Amyloid* † is, when dry, a cartilaginous, but moist, gelatinous, clear, transparent body, soluble in boiling water, strong acids, and caustic alkalies, but not in ether and alcohol in a concentrated state. It is coloured blue by iodine, and the combination is soluble in water, giving it a golden-yellow colour. It is found only in the layers of the primary cell-membrane. There is no chemical analysis of this substance. It has been found at present only in the cotyledon-cells of *Schotia latifolia*, *S. speciosa*, *Hymenæa Courbaril*, *Mucuna urens*, *M. gigantea*, and *Tamarindus indica.* Perhaps many of the observations of Hugo Mohl belong to this substance.

3. *Vegetable Jelly* (Vegetable Mucilage, in part, of the chemists, Bas-

* See Hugo Mohl, Some Observations upon the blue Colouring of vegetable Cell Membrane, through Iodine. Flora, 1840.

† See Poggendorff's Annalen, 1839.

sorin, Salep, *Lichen carragheen* (*Chondrus crispus*) Gelin). This substance, when dry, is horny, or cartilaginous; when moist, it swells up and becomes gelatinous, and diffuses itself perfectly through cold pure water. When pure it is clear, and is dissolved by (perhaps only diffused in) both cold and hot water, and also in caustic alkalies; it is, perhaps, chemically changed in pure acids. It is insoluble in fixed and volatile oils, ether, and alcohol, and is not coloured by iodine. It passes, on the one side, through various transitionary bodies into cellulose (through the cell walls of the *Fucoideæ*), and into amyloid (through some kinds of horny albumen), and on the other side into starch (through the jelly of the orchis tubers), and, in many ways, into gum and sugar. None of these bodies have been analysed, so far as I know, and reduced to chemical equivalents.

Vegetable jelly forms the cell-walls of most *Fucoideæ*, the albumen of the *Cæsalpineæ*, and, in part, the so-called horny albumen (*Albumen corneum*). It is also, like gum, found in the contents of the cell. It is especially abundant in the cells of the tubers of our indigenous *Orchideæ* and in the *Cactaceæ*, filling large individual cells, which at first often exhibit upon their surface a granulated aspect: in the *Cactaceæ* they are often distinguished by a vermiform twisted line. It is also seen, as a secretion, in the gum-receptacles, especially in tragacanth; and a part also of the intercellular substance seems to belong to it.

In the same way as in animal chemistry, we distinguish between gelatinous substances and gelatine; so does Kützing (Phycologia generalis, p. 32.) distinguish gelin from vegetable, which last, by boiling, passes into the first. Vegetable jelly will also, by long boiling, pass into mucilage (schleim). These three substances appear to me to be hydrated states of a common basal principle. Kützing's horny gelin (said to contain nitrogen) and his gelacin (through hydrochloric acid coloured verdigris-green) appear to be only gelin contaminated by foreign bodies. At any rate, the experiment of determining the nitrogen which was given off in the form of ammonia, during the combustion of an entire plant, to be a constituent of a particular substance, is too coarse to be admitted as of any worth at the present day.

Whether pectin and pectic acid ought to be admitted under this head appears, according to Mulder's experiments, doubtful.* He gives the formula C 12, H 8, O 10. They appear to be more nearly related to malic acid, and form, perhaps, transitionary bodies between the organic acids and the indifferent secretions. The analyses, by Mulder, of the carragheen moss (*Chondrus crispus*), the mucilage of the quince and the marshmallow, and of tragacanth gum, vary too much to allow of even a common formula. The inquiry must not be disregarded, how the separation of the various substances intimately mixed, as in the carragheen moss and tragacanth gum, can be separated, so as to yield a pure substance fitted for chemical analysis. That pectin belongs to the substances employed in thickening the cell-walls, is a fiction which no one microscopical observation of ripe or unripe fruits, or of roots containing pectin, supports.

4. *Starch* (Amylum, Amidon, Lichen-starch). When dry, it is tolerably hard, cracking between the fingers: when moist, somewhat gelatinous: dried from its solution, at first a trembling jelly, at last as brittle as glass: when pure, constantly clear (even in lichens): when perfectly pure and fresh from the plant, gradually dissolving in water. This solution may, perhaps, be regarded rather as a diffusion through water,

* Poggendorf, Annalen, b. xlvi. (1838), p. 432.

as the so-called solution does not penetrate through cell-membranes. In the plant it is ordinarily defended from this solution by the action of wax, albumen, mucus, and the like. It is easily soluble (diffusible) in boiling water, acids, and alkalies; insoluble in alcohol, ether, volatile and fixed oils, and is coloured blue by iodine in the most dilute solution.* It appears, through modifications such as lichen-starch, to pass into amyloid, and, through the body discovered by Henry in mace, into cellulose vegetable jelly, and perhaps also gum. On its chemical composition the most distinguished chemists, Berzelius, Liebig, and others, are all agreed: C 12, H 10, O 10. It forms the cell-wall in the asci of Lichens; and in some, as the Iceland moss (*Cetraria islandica*), it is found in the external layer of the thallus. It is also present, forming the contents of the cells.

### A. *The Nature of Potato Starch.*

The ordinary potato-starch of commerce consists of a somewhat coarse, glistening, white powder, intermixed with larger pieces. On rubbing it between the fingers, it pulverises more finely, but is somewhat hard to the touch, and grates between the teeth. When moistened it cakes together in larger masses, and does not fall to pieces again on being re-dried. When, however, this starch, after a long-continued extraction with cold water, has been thoroughly purified with alcohol and ether, it forms an extremely fine, glistening powder, which will not continue to adhere together on being moistened and dried. Some considerable time is required to purify the starch perfectly, and the fluids used for its purification continue for a long time to exhibit traces of albuminous matters and of fats. The very various views that have been entertained regarding the chemical relations of starch appear to me specially to arise from the fact, that experiments are never made with perfectly pure, but with variously adulterated, specimens. Payen and Persoz were the first who seem to have thought of thoroughly purifying starch before they used it, and the consequence was that the result of their experiments wholly differed from those of others, and showed that starch was a perfectly homogeneous vegetable substance.

When magnified 100 times, the separate granules of starch appear like small, solid, invariably ovate corpuscles. Deviations from this form are, comparatively speaking, very rare. In starch that has been freshly extracted from the potato, we recognise most distinctly a small black spot by its pointed extremity: this is Fritsche's nucleus. It is only very rarely, and when very strongly magnified, that it appears as a speck in the potato, filled with such a thin substance as to allow of our regarding it as an indentation, or rather as a small cavity, in the denser mass. This, however, is made much more clearly evident in the starch extracted from the bulbs of some of the *Liliaceæ*, and is established with perfect certainty on comparing it with various other kinds of starch. Around this so-called nucleus there appears, sometimes paler or blacker, or sometimes closer or further, a large number of lines, which at first pass circularly round the nucleus: further on they describe more of an oval course, as they elliptically enclose the nucleus like a focus. The space enclosed by two such lines appears sometimes lighter, sometimes darker, often strikingly clear at separate spots; and an experienced microscopic observer will soon recognise layers of different density, and that the

* Iodide of starch is not more soluble in water than starch, and insoluble in acids.

external ones are generally clearer than the internal, which, in fresh starch, often appear almost gelatinous. The dark lines do not intersect the line of the external circumference in any one of the granules; and, however close they may lie to each other at the pointed end, every line perfectly returns to itself. On turning a single granule with deeply blackened lines under the microscope, which may be easily done by the addition of a drop of water, which will occasion a small current, we shall see that the lines, when considered from all sides, remain equal, and always encircle the nucleus in the same manner. From this it follows that they cannot be mere markings upon the surface, but the surfaces of contact of many hollow ovate scales laid around each other: from this the whole granule is composed. Sometimes on making a fine section, with a sharp razor, from a potato containing much starch, we may succeed in seeing several granules of starch sharply intersected under the microscope; and we may thus perfectly convince ourselves that the layers towards the interior are in general more aqueous and gelatinous, and that those towards the exterior contain less water and are tougher.

Perfectly dried granules exhibit a smaller number of lines, although they are frequently more strongly marked; and we may often perceive that each broad black line corresponds to a thin layer of air. On suffering starch to remain for any length of time in gum water, the lines gradually will disappear more and more; and on drying it with the gum, until the whole forms a perfectly tough mass that may be cut with a knife, we may easily obtain a great number of sections by cutting off small chips, and even have several thin discs from a single granule. In the latter we discover a tolerably homogeneous substance, having in the centre a somewhat irregular indentation, which has naturally been occasioned by the drying up of the interior aqueous layers.

On treating starch under the microscope with sulphuric acid, very different phenomena appear, according as to whether the acid is stronger or weaker, and the action rapid or slow. On the rapid action of strong acid, the granule is immediately affected from the point where it is touched by the acid; it becomes distended, and gradually dissolves,—a process that is quietly continued to the other end of the granule. We often see granules which are quite dissolved at one end, while the opposite end is still sharply defined, showing even a nucleus and layers. The whole mass of the granule is quite uniformly affected, without the outer layers being torn open, or the fluid contents escaping. In a slower action of the acid, two different forms of solution occur alike frequently, depending probably upon the different degree of concentration of the acid. In dilute acid the granule becomes gradually transparent and gelatinous; swells up, but in such a manner that it first exhibits an impression at one side, and by degrees (swelling up less at the compressed side than externally) assumes a complete cup form, and is at last gradually dissolved from the margins. The other form, exhibited by the slow action of the very concentrated acid, consists in the nucleus passing over into a decidedly recognisable air-bubble. This expands, causing one or two jagged rents in the interior of the granule, which gradually inflates and becomes gelatinous, whilst the lines disappear, as far as they are touched by the rent, until the whole granule is rendered invisible (dissolved). The first action of the sulphuric acid appears to be, that water is withdrawn from the inner layers; and this appears further confirmed by the action of dry heat.

On heating potato starch upon a small plate, to such a degree that only a

minute portion, immediately in contact with it, assumes a yellowish colour, we may easily trace, under the microscope, every possible stage of transition in the gradual change ; which is very remarkable, and affords the best explanation of the structure of the starch granule. The first action here is naturally one of drying, by which the so-called nucleus is converted into an air-bubble, appearing so characteristic that we can thereby distinguish the use of dry heat, as, for instance, in the *Mandiocca farinha*, in Sago, &c. The individual layers simultaneously separate, and, in consequence of drying out, the lines of separation become sharper, blacker, broader, and even recognisable broader or narrower layers of air ; the layers hang closer together at some places than at others, and larger or smaller spaces are formed. By degrees the separate layers peel away from each other, like the scales of a bulb, whilst an actual fusion (conversion into gum) takes place at individual points.

If we continue the action of water, heated gradually to the boiling point, a change at first takes place, which is very similar to what has been just described with reference to sulphuric acid. It is only in the latter stages that the phenomenon is so far different, that the cleft in the interior is gradually converted into a large cavity, when the whole swollen granule looks like a compressed thick-skinned bag.

By degrees the outlines grow more indistinct ; but the paste-like mass, consisting of a granule, continues clinging together; and, on looking under the microscope at the thinly boiled paste mixed with water, we may, by means of iodine, recognise the separate and inflated granules, whilst the water added is never coloured blue. I have not been able to continue the boiling during several days, but I think I may venture to conclude, from my own experiments, that starch may take up a large quantity of water, and thus swell to a large volume (although even this seems to have its limitations), but that it never can be properly dissolved either in cold or boiling water.

I will here finally mention the treatment of starch with cold water. If starch be rubbed up, for the period of half an hour, in a mortar, with double the volume of water, we obtain a viscid, almost stiff, salve, capable of being drawn into threads. A large number of the granules then appear under the microscope, to be crushed in various ways, torn and broken up, partly ground into small flakes. The inner aqueous layers are pressed and combined with more water by friction, as it appears, exhibiting a finely floccular or granular, but connected, mass, which is coloured blue by iodine, whilst all the actual fluid round (the water) remains wholly uncoloured.

All these experiments were frequently repeated with different impure specimens of starch, such as are commonly bought, but all of the same kind ; and the results were, in every case, essentially the same. Iodine was always used in these experiments, and there never was the most remote indication of there being any part in the starch granule which was not equally coloured by it. There never occurred the slightest appearance, in these experiments, to refute the easily tested fact, that the layers of starch granules are more aqueous in proportion as they lie further to the interior : nor was the unimportant point refuted, that there were slight differences in the external layers, arising from the adhesion or infiltration of some few traces of albumen, fat, or wax ; these differences merely resulting in a longer or shorter delay of the action of the solvents. The same experiments were constantly repeated with purified starch, in order fully to test the correctness of the last-named facts.

It will now be easily apparent from what has been said, that without a simultaneous application of the microscope and chemical re-agents it is utterly impossible to think of a true and fundamental knowledge of starch. Starch is gradually dissolved in the full-grown potato, so that after three months there is scarcely a trace of it to be met with in that vegetable, even where it is in a perfectly sound condition. This solution is most essentially different from all others that we are able to bring about. The individual granule retains to the last moment its solidity, and is only gradually attacked from the exterior towards the interior; the extremities of the longitudinal sections offering the greatest resistance, on which account the granule after a time resembles a knotty twig, owing to the prominent appearance of the rest of the layers. The same thing occurs in the germination of the cereals, and in the solution of starch which takes place through diastase, but only at a temperature of 70° C.,* which corresponds entirely in form with the solution by sulphuric acid, and has been referred by chemists, with an inconceivable degree of superficial carelessness, to the process in living plants.

## B. *On the Occurrence of Starch in various Forms in the Vegetable Kingdom.*

We have only one treatise, and that by Fritsche (Poggend. Ann. vol. xxxii.), deserving of notice, on the differences of starch in different plants; and this, with some few inconsiderable additions, has been made use of by Meyen in his Vegetable Physiology. For the rest, this work appears to have met with very little attention; for when we read a passage to the following effect in one of the most recent works, "Starch appears in the form of small spherical corpuscles," (Endlicher und Unger, Grundzüge der Botanik,) we may easily see that the authors have neither made original observations on the subject, nor even read anything regarding it. The forms of starch are exceedingly various, and often, as Fritsche remarked, so characteristic, that we may easily, by means of the starch, determine the plant, at any rate with reference to its genus and family. I subjoin the following tabular list of the forms with which I am acquainted.

### I. Amorphous Starch.

Hitherto I have found amorphous starch only in two phanerogamic plants, it occurring then paste-like in the cells, as in the seeds of *Cardamomum minus*, and in the bark of the Jamaica Sarsaparilla. In the case of the latter, however, it is not improbable that the method of drying by the fire, common in the preparation of Sarsaparilla, may change the character of the starch. The paste is most frequently found in abnormally red roots, and more seldom in the yellow; neither of which, however, have hitherto been esteemed in commerce as varieties of the Jamaica Sarsaparilla.

### II. Simple Granules.

The majority of plants exhibit perfectly simple individual granules, among which doublets and triplets only occur as exceptions. We may further distinguish the following groups: —

* A temperature that would kill every vegetable embryo.

### 1. *Roundish Bodies.*

*A.* With the central cavity, Fritsche's nucleus, apparently wanting.

1. Quite small, almost spherical, granules, occurring almost everywhere in the vegetable kingdom, from time to time, as cellular contents; for instance, in Carrots, in cambium, in the winter; in leaves, as the bearers of Chlorophyll, &c.

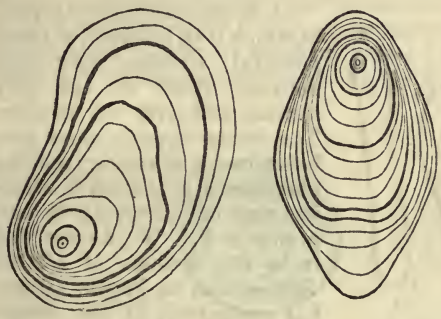
2. Large, irregular, knobby, often truncated multangular granules; as, for instance, in the bulbous buds of *Saxifraga granulata*, in the spurious tubers of *Ficaria verna*.

*B.* With small roundish central cavities.

*a.* With a perceptible laminated formation.

3. Very large, rough, granules, deformed as it were, found in the pith of the *Cycadaceæ*. There are somewhat similar granules in the subterranean leaves of *Lathræa squamaria;* in these the inner layers form an ovate granule, almost similar to those of potato starch: the few external ones, on the contrary, are so irregular, and generally so disproportionally thickened at one or two sides, that the whole granule assumes a broadish triangular figure.

6.



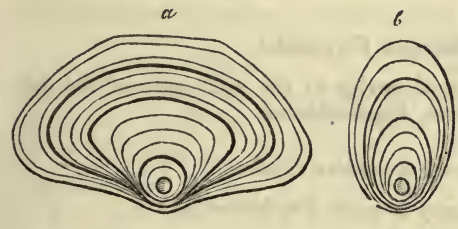
4. Ovate granules. In the potato (fig. 6.).

5. Mussel-like granules. In the bulbs of the larger *Liliaceæ*, as in *Fritillaria*, *Lilium* (fig. 7.), &c.

6. Almost triangular in tulips.

*b.* With an indistinct or deficient lamellated formation.

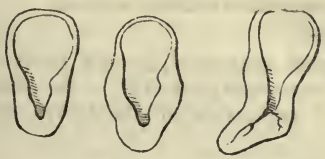
7.




7. Rounded-off polyedric granules. In the albumen (perisperm) of *Zea Mays*.

8. Sharp-edged, polyedric, very small granules. In the albumen of *Oryza sativa*.

8.



*C.* With an elongated central cavity.

9. Roundish or oval granules, in a dry condition, generally showing a star-like cleft in the inner layers. In the *Leguminosæ*, as in the seeds of *Pisum*, *Phaseolus*.

*D.* Perfectly hollow, apparently cup-like, granules.

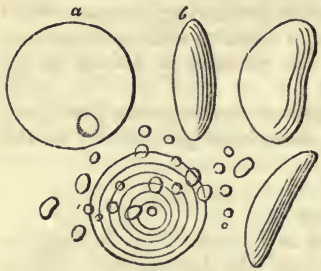
[6] Granules of starch from the potato, the layers being copied true to nature.

[7] Granules of starch from the bulb of *Lilium bulbiferum*. The layers are faithfully delineated: *a*, from the surface; and *b*, a lateral view.

[8] Granules taken from the rhizoma of *Iris pallida*, with a large central cavity.

10. Very marked in the Rhizoma of *Iris florentina*, and in the kindred species (fig. 8.).

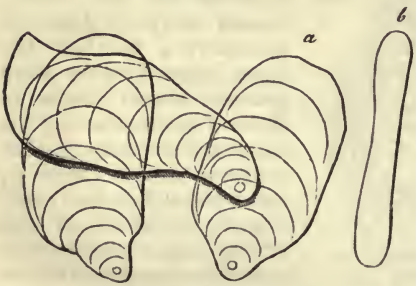
9.




2. *Flatly-compressed lenticular Granules.*

11. Sometimes with, sometimes without, a decided lamellated formation; sometimes with a central, or excentric, or less rounded, or more elongated, or radiated torn-up cavity. In the albumen of *Triticum, Hordeum, Secale* (fig. 9.).

10.




3. *Perfectly flat Discs.*

12. With more distinct layers, in which it is, however, at times doubtful whether they pass entirely round, or are only menisci laid over one another. The former appears to me probable, owing to analogy, and the phenomena presented in roasting and on dissolving in sulphuric acid. We do not find it in the rhizoma of all the *Scitamineæ*, as Meyen attests, but exclusively in the *Zingiberaceæ* Lindl.; neither in the *Cannaceæ*, nor in the *Marantaceæ* (fig. 10.).

4. *Elongated Corpuscles.*

13. With an elongated central cavity in the milk-juice of the indigenous, and a few of the tropical, *Euphorbiaceæ.*

5. *Perfectly irregular Bodies.*

14. In the milky juice of many tropical *Euphorbiaceæ.*

III. Compound Granules.

Here we only find simple granules, by way of exceptions, in the plant, or part of the plant.

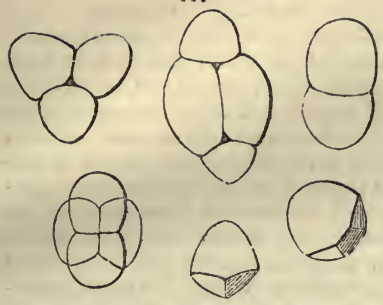
1. *The separate Granules in the Composition without evident central Cavity.*

15. Compounded, according to the simplest types in 2, 3, or 4 in the rhizoma of *Marantaceæ* (West Indian Arrow-root) (fig. 11.). In the tubers of *Aponogeton;* in the thickened vagination of the leaves of *Marattia;* in the root of *Bryonia.*

[9] Granules of starch from the albumen of the seed of *Secale cereale: a* is seen from the surface, *b* from the edge. The difference of size, without any intervening stages, is striking in *Secale, Triticum, Hordeum,* &c.

[10] Granules of starch from the rhizoma of *Curcuma leucorrhiza* (East Indian arrow-root). Very flat discs seen at *a* from the surface, and at *b* from the margin.

11.



16. Generally regularly, seldom irregularly, composed of from 2 to 6. In the bark of the roots of the various sorts of *Sarsaparilla.*

2. *The separate Granules in the Composition having a distinct central Cavity.*

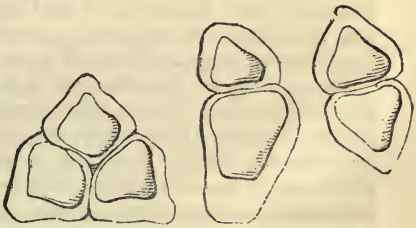
*A.* All the parts of the granules nearly of the same size.

17. United, according to simple types, from 2 to 4. The central cavity small and roundish. In the tubers of *Jatropha Manihot.*

18. Combined from 2 to 4, according to simple types. The central cavity large and very beautiful, opened in a star-like form. In the cormus of *Colchicum autumnale* (fig. 12.).

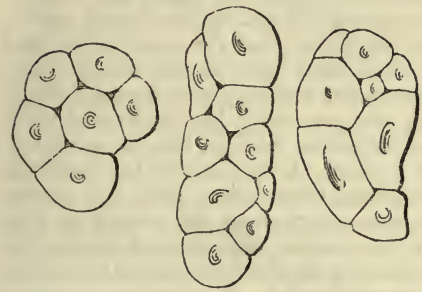
12.

13.



19. Combined according to simple types from 2 to 4. The separate granules quite hollow, apparently cup-shaped. A marked form occurs in *Radix Ivarancusæ* (*Anatherum Ivarancusæ*) (fig. 13.).

14.



20. Firmly combined, from 2 to 12 in number, in very irregular groups. In the rhizoma of *Arum maculatum* (fig. 14.).

21. A large number (often as many as thirty) of small roundish granules, very loosely rolled together. Frequent, as, for instance, in the stem of the *Bernhardia dichotoma.*

[11] Granules from the rhizoma of *Maranta arundinacea* (West Indian arrow-root) Composed of from 2 to 4 granules, the separate parti-granules always exhibit the smooth connecting surfaces.

[12] Starch granules from the cormus of *Colchicum autumnale.* The separate granules are quite similar to those in the seeds of the *Leguminosæ*, but generally composed of from 2 to 4, with very beautifully radiated opened central cavities.

[13] Starch granules from the rhizoma of *Anatherum Ivarancusa* (*Radix Ivarancusæ*). The separate granules with large central cavities, as in *Iris florentina*, but composed of from 2 to 3 combined.

[14] Starch granules from the subterranean stem of *Arum maculatum*, irregularly composed of many grains, each granule having an indistinctly defined central cavity.

*B.* Many smaller granules grown together upon one larger one.

22. In the pith of *Sagus Rumphii*, &c., generally in the sago.

Starch is the most generally distributed substance in the vegetable kingdom. I am not acquainted with any plant which does not, at some season of the year, at least at the period when vegetation is inactive, contain more or less starch, frequently only in individual granules in the cells, and frequently entirely filling them in grains of the most different size. The starch granules adhere quite adventitiously, by means of mucus, to the cell-walls. The umbilicus (hilum), by which the starch granules are said to be attached to the wall of the cell, is an error on the part of Turpin. The largest granules do not appear to exceed 0·05 of a line in their longest diameter. The starch is mostly readily obtained by bursting the cellular tissue, and by washing it from the plant; occasionally, however, it cannot be thus obtained, as, for instance, when it occurs combined with much mucus, as in *Hedychium;* the starch in *Maranta arundinacea* (Arrow-root) appears to be the purest. We certainly do not say too much when we assert that starch constitutes the most important, and the almost exclusive, food of two-thirds of all mankind. It is certainly contained in all plants, but not always in such a manner as to be sufficient and suitable for nutriment, and sometimes, too, indivisible from other unpalatable admixtures, as, for instance, in the horse-chestnut. Certain parts of plants contain it in the largest quantity, namely, the albumen of seeds (the *Cerealia*), the cotyledons of the embryo (*Leguminosæ*), the medulla, or pith of the stem (*Cycadeæ* and *Palmæ*) * bulbs (*Liliaceæ*) †, the tubers, root-stocks, and roots of very different families.‡ It occurs in smaller quantities in the bark and the alburnum of trees in winter, whence the inhabitants of the Polar regions are able to bake the bark of trees as bread.

I must not omit to make mention of an error, which is unfortunately too often repeated, and which may thus lead to much confusion, especially in physiology. Decandolle believed that he had proved that 100 lbs. of potatoes would yield 10 lbs. of starch in August, 14½ lbs. in September, 14¾ lbs. in October, 17 lbs. in November, 13¾ lbs. in April, and again 10 lbs. in May. From this it was concluded that the quantity of the starch in the potato increased and diminished again during this interval of time,—a most erroneous idea, which has unfortunately been too often repeated in recent times. It may, however, easily be conjectured that such per-centage calculations can only give relative, but no absolute, quantities for any plant, or part of a plant. Granting that Decandolle's calculation is correct, it says nothing more than that the weight of starch gradually comes to stand in the same relation to the weight of the potato as 10, 14½, 17, &c., to 100; but whether this changed relation is to be sought in the change of the quantity of the starch, or in the diminution of other substances, is not even indicated. It is rather obviously probable that in this case starch is neither formed nor destroyed, but that the aqueous contents of the potato decrease by evaporation, and again augment by absorption on the revival of vegetation.

*Historical Sketch.*—Starch was known even to the ancients. (Ἄμυλον διὰ τὸ χωρὶς μύλου κατασκευάζεσθαι, Dioscor.) Leeuwenhoek was the first who examined it in plants, in wheat and beans; and Stromeyer sub-

* As sago, from *Cycas revoluta, Sagus Rumphii, farinifera*, &c.

† *Lilium camtchaticum*, in Greenland, &c., is a source of food.

‡ Potatoes, from *Solanum tuberosum;* Cassava, from *Jatropha Manihot;* Taroo, from *Arum esculentum* (*Colocasia macrorhiza ?*), &c.

sequently discovered the property possessed by starch of being coloured blue by iodine.

Few substances have been so comprehensively treated of as starch, and few have been more imperfectly and unsatisfactorily known, — this arising solely in consequence of neglect or superficiality in microscopic investigations. A very clear and comprehensive report of Poggendorff upon the numerous works, up to 1836, written on this substance, may be found in Pogg. Annal. der Chem. und Pharm., vol. xxxvii. p. 114., &c. The result of the whole is concisely summed up in these striking introductory words: —

"No substance has been more investigated, and is yet less known, than starch. It affords a striking proof of the diffuse manner in which a subject may be treated if it fall into improper hands. After ten years' investigations, in which the most various views have been set up on the nature of starch, and when all its characteristics as a proximate vegetable substance have been discussed, we are little or nothing in advance of the old point of view; and although, perhaps, we may not be wholly without some extension to our knowledge in secondary points, we are still entirely without fundamental grounds in proof of our having arrived at the truth."

Since Poggendorff wrote these words, eight years have elapsed. Innumerable works upon starch have been published by chemists and vegetable physiologists; and, on testing more exactly what has been done in Endlicher's and Unger's Rudiments of Botany, we find that the labours of the last eighteen years are lost, even as far as relates to the more general knowledge of this substance, whilst the whole confusion in the literature of those eighteen years may be found reflected in the few lines of those writers, who evidently were not able by their own elementary investigations to avail themselves with discrimination and judgment of the extensive literature opened to them. The diametrically opposite views of Fritsche and Raspail are so blended together in the most extraordinary manner, that the confusion is beyond all description.

There are two views upon the structure of starch granules decidedly opposed to each other, on the assumption or rejection of which the chemical judgment passed upon this substance must essentially depend. The first, originating with Leeuwenhoek, and subsequently further developed by Raspail, tends to prove that the individual starch granules consist of a tough sac, and semi-liquid, easily soluble contents (Dextrin), and that both parts are chemically different. This view effected the refutation of the diffuse works of the French chemists, who, although they differed upon words and secondary points, yet agreed in the main that starch was no proximate vegetable matter, and that the starch granule was composed of substances differing considerably in a chemical point of view. Among these may be reckoned especially the works of Guibourt, those earliest written by Payen and Persoz, and those of Guérin-Varry. Finally, after giving many proofs of their incapacity to compose an unprejudiced and *thorough* analysis of organic substances, Payen and Persoz came to the conclusion, "that starch purified from all extraneous matter was a simple, homogenous, proximate vegetable substance." Raspail's view was entirely given up, and the structural relations of starch not more thoroughly pursued. Such was the state of things in France. In Germany, starch was first more accurately examined by Fritsche*, and by aid of the microscope, which is indis-

* Poggendorff's Ann. vol. xxxii. p. 129. (1834).

pensable in an investigation of this kind. His results form the second hypothesis upon the nature of starch, which we may oppose as the views of *German vegetable physiologists* against those of the *French chemists.* According to the former, starch is composed of layers ranged over one another, all consisting of the same chemical substance. The external layers are less easily soluble in water, owing to their saturation with foreign substances. In the interior there is an extremely small nucleus, which appears, by its behaviour during the action of hot water, acids, and alkalies, neither to be starch, gum, nor sugar. This is more especially the case with potato starch, but the starch granules of the curcuma roots appear to differ somewhat from this, exhibiting elongated flat discs, while those of the cereals have lenticular bodies. Subsequent observation (especially on the part of Meyen) has shown abnormally-irregular forms in the milky juice of the *Euphorbiaceæ.* And here the theory rests, as far as the main point is concerned. There has as yet been no thought of a more exact investigation of the structural signification of the chemical relations, or of a comprehensive comparison of the different kinds, of starch in various plants. The whole of this question has been condensed in Endlicher and Unger in the following improper manner:—"Amylum granules consist of a more or less solid (?) nucleus, around which layers of solid (!) consistency are by degrees eccentrically deposited, admitting sometimes even of being peeled off. (?) On the external case (?) of the amyhum granule being burst, the interior will dissolve even in cold water, and that about 0·413 of the whole granule. The chemical character of the nucleus is not essentially different from that of the layers which either partially or entirely invest it. (!) Iodine colours both parts in like manner, blue! . . . . . Concentrated (?) mineral acids dissolve the amylum granule, boiling water occasions only an enlargement in its size by means of absorption, and this often gives rise to a cleft in the *external layers* (!) through which the softer *nucleus* (!) is expressed. The probable special substance of the *nucleus,* the so-called *dextrin,* consists of *gum* and *sugar.*" (!!!)

By way of historical references we may recommend Poggendorff, Annalen, vol. xxxvii. (1836), p. 123.; Meyen's Physiologie, p. 190.; Mulder's Physiol. Chem. Moleschott, p. 215.

5. *Gum* (Arabin, Dextrin, Vegetable Mucilage in part). In a pure state it is clear; when dry, brittle like glass; easily soluble in water, and also in dilute acids; not soluble in ether, alchol, and volatile and fixed oils. The action of alcohol makes it horny, and it is coloured pale-yellow by iodine. It passes through cerasin and some so-called varieties of mucilage into vegetable jelly; it borders through dextrin on starch. The analysis of gum Arabic by Berzelius gives the formula, C 12 H 11 O 11; of gums Arabic, Senegal, and Java, by Mulder, C 12 H 10 O 10.

It is found in a state of solution in the interior of cells, or as a secretion in the great gum canals, and not unfrequently mixed with vegetable jelly, and is frequently, through foreign substances, coloured yellow or brown, a condition in which it is almost always found when collected for commercial purposes. Some groups of plants are distinguished by the great quantity of gum they produce, as the *Mimoseæ* and the *Cycadeæ.*

The substance called dextrin, and which can be formed through the action of dilute sulphuric acid, diastase, &c., on cellulose or starch, agrees with gum in many points, and especially in its elementary composition. It seems to be a substance of more importance than gum. According to Mulder, the greater part of what has hitherto been called

gum is dextrin. Some time ago I advanced the opinion that dextrin must be present in plants where so much cellulose and starch was dissolved and changed. Soon after, Mitscherlich pointed out the actual presence of this substance in the sap of many plants. The principal difference between gum and dextrin consists in the fact, that the latter, by the action of dilute sulphuric acid or diastase, is converted into grape-sugar, while the first is not. Gum apparently originates in the plant from dextrin, and not as a special product of secretion; whilst dextrin is present in all the juices of the plant, and especially where cells are about to be formed, and appears to be the formative matter of the plant. Countless almost, however, are the modifications of dextrin, through vegetable jelly, till it forms cellulose.

6. *Sugar.* In a solid state, and entirely pure, sugar is crystalline, clear, and easily soluble in water. In some states it is uncrystallisable, and then, through foreign substances, coloured yellow or brown. It is slightly soluble in alcohol, but not in ether, volatile and fixed oils. It mixes with a solution of iodine. The analyses give, according to various modifications, various results:—

| | C | H | O |
|---|---|---|---|
| Anhydrous salt of sugar, with oxide of lead, according to Berzelius and Liebig - - | 12 | 10 | 10 |
| Crystallised cane sugar, according to Gay-Lussac, Thénard, Berzelius, and Liebig - | 12 | 11 | 11 |
| Grape sugar, from a crystallised compound with common salt, according to Brunner - | 12 | 12 | 12 |
| The same from grapes, honey, and starch, according to Saussure and Prout - - | 12 | 14 | 14 |

Sugar, which is principally distinguished by its sweet taste, is by various modifications, and in every case through inulin, connected with the other bodies, but of the transitionary conditions we know but little. It presents itself very widely in the vegetable kingdom, and especially where starch and the other substances are developing or are dissolved, as in unripe peas and cereal grains; and the early sap of trees, as of the maple and beech. It is found in greater quantities, and in a more permanent form, in the stems of grasses, as the sugar-cane and maize, and the *Holcus saccharatus;* in fleshy roots, as in the carrot and beet; and in juicy fruits, as the pear and apple, gooseberry and currant. Naturally it is found dissolved in the plant, but when it becomes excreted it assumes the forms of crystals, as in the nectaries of plants (ex. gr. *Fritillaria imperialis*). Mannite, the sugar of manna, does not belong to this series of compounds. It is only the product of the decomposition of the sugar cane. Its formula is $C\,6\,H\,7\,O\,6$. According to Mitscherlich, the *Tamarix gallica*, which yields manna, contains in its tissues no mannite, but cane sugar.

7. *Inulin* (Dahlin, Calendulin, Synantherin, Sinistrin). It is obtained from the tubes of the dahlia by simply washing. It is a powder with fine grains; the grains clear, easily soluble in boiling water, from which it separates, on cooling, in a granular form. It is insoluble in ether and alcohol, coloured yellow by iodine. Cold water makes the grains to disappear to the eye under the microscope, because their refracting power is similar to that of water. Hence the erroneous assertion of Link and Meyen, that inulin is always in solution in plants. Crookewitt found that inulin, by being boiled in water fifteen hours, was converted into an

uncrystallisable sugar. According to the researches of Mulder and Crookewitt (Liebig's Ann. Bd. 44. S. 184.), inulin from the dahlia, helenium, and the dandelion, in a pure state, consists of C 12 H 10 O 10. It is thus isomeric with sugar and starch. Inulin has been found in many places where formerly starch was supposed to be present, as in tubers and fleshy roots (ex. gr. *Inula Helenium, Dahlia variabilis*), and is probably a very widely extended substance.

8. *Fixed Oils and Wax.* The great peculiarities of these physically and chemically varying substances is the property of leaving upon paper a transparent spot, and not adhering to water. Their colour is very various; clear, yellow, and brown.

*A. Fats* (Fixed Oils). They are very widely distributed, and frequently take the place of starch, as in the cotyledons of the *Cruciferæ* (ex. gr. the species of *Brassica*), of the *Synanthereæ* (as *Helianthus annuus, Madia sativa*) and many other plants. They are found in the juices of the fruits and roots; and there is, perhaps, no plant, or no part of a plant, that does not contain a small quantity. The most common fats in the vegetable kingdom are elain and margarin, which are formed, according to Mulder, of glycerin (C 3 H 2 O), and elaic acid (C 44 H 40 O 4 + HO), and margaric acid (C 34 H 34 O 3 + HO). Elain is fluid, margarin solid; and the two, mixed in various proportions, form the fixed oils found in plants. Besides these, there are peculiar oils, such as the cocos and muscat butters, palm and bay-berry oils. They form soaps with the alkalies, which are soluble in water. Alone they are insoluble in water, in ether and alcohol gradually soluble, and in volatile oils perfectly so. Of their changes into the other bodies mentioned, we know nothing; at the same time it cannot be doubted, from what we know of the phenomena of germination in oily seeds.

*B. Wax.* This substance, which is distinguished from the oils and fats through its perfect insolubility in cold alcohol, and its brittleness, is found extensively in the vegetable kingdom, and plays an important part. There are few plants that do not present traces of it upon their surface. In all those plants and parts of plants called hoary, the delicate bluish bloom consists of a thin layer of very small wax granules. This layer is much thicker in the fruits of the order *Myriceæ*, of *Croton sebiferum, Tomex sebifera, Rhus succedaneum*, the leaves of *Encephalartos*, the bracts of *Musa paradisiaca* and *Strelitzia farinosa*, the stem of *Ceroxylon andicola*. In plants generally it appears to be the basis of the chlorophyll; and in many families, as, for instance, the *Balanaphoreæ**, it forms the entire contents of the cells. It is found in large quantities in the milky juice of the *Galactodendron utile*, forming the Galactin of Solly. In wax two proximate principles appear to be present, *myricin* (C 20 H 20 O), insoluble in boiling alcohol, and *cerin* (C 10 H 10 O), soluble in boiling alcohol. Wax is decidedly formed by bees out of sugar. A form of wax exists, according to Avequin (Ann. de Ch. et de Phys. Oct. 1840, p. 218.), in the sugar-cane, which sometimes passes into sugar, and which is sometimes formed out of sugar. The wax, which is combined with chlorophyll, appears to be formed from starch, perhaps from inulin (see Mulder, Physiol. Chem. Moleschott, p. 253.). The composition of the last form of wax, obtained from apple-peel, according to Mulder, is C 40 H 32 O 10, but in most green leaves C 15 H 15 O. In every case it was found poor in oxygen. The majority, however,

* See Göppert on the structure of the *Balanaphoreæ*, in Act. Acad. Leopold. Carol. Nat. Cur., vol. xviii. Supplem. pp. 236. 253.

of the forms of wax have not been sufficiently examined. According to the first formula, 10 equivalents of starch (C 120 H 100 O 100) forms 3 equivalents of wax (C 120 H 96 O 30), with the loss of 2 HO and 66 O. According to the second formula, 5 equivalents of starch + 10 HO = C 60 H 60 O 60, which, by losing 56 O, is converted into 4 equivalents of wax, C 60 H 60 O 4.

§ 10. Another class of substances is found in plants, which neither exist in the cell-walls, nor are the cell-walls formed from them, but nevertheless their presence is necessary for the simplest processes of vegetation. They are composed of Carbon, Hydrogen, Nitrogen, and Oxygen, to which are sometimes added Phosphorus and Sulphur. I call them by the collective name Mucus (*Schleim*); the chemists give them various names, as Albumen, Gluten, Gliadin, Zymom, Gelatin, Diastase, Gluten vegetabile, Legumin, &c.

In all the vital cells of plants, besides the substances mentioned in the last section, there is found a semi-fluid or liquid granular matter, of a pale yellow colour, sometimes entirely fluid, sometimes solid, and which, through the action of alcohol, becomes entirely granular, fibrous, or semi-membranous; which is coloured dark brown by iodine; and which, according to all observation, is a multiform, changeable substance. Many modifications of this substance have been separated from plants by chemists, to which they have given the above names, but which are perhaps seldom pure, and often formed during the process of separation. All of them are characterised by the possession of nitrogen, and also by their action (11.) on the previous substances (9.). They are sparingly present, or are absent altogether, in those parts of plants which contain starch, and which do not easily pass into fermentation, as the tubers of the potato, the fruit of the rye, and the rootstock of the arrow-root plant (*Maranta arundinacea*); but in parts of plants which easily ferment they are found in large quantities, as in good wheat, the juice of the grape, &c.

In the youngest cells of plants, the mucus (*Schleim* of Schleiden; protein of chemists*) presents itself as a slight covering over the whole inner surface of the walls of the cells. (See this work on the Motion of the Sap in Cells.) In the seeds of *Leguminosæ*, this substance is found in the same cells which contain starch, but in smaller and larger quantities in especial cells, and sometimes apparently filling them entirely. Thus, in the grains of the *Cerealia*, the layer of cells immediately under the coats of the seed are almost exclusively filled with the mucus, whilst the remaining cells of the albumen (perisperm) contain starch, with only a small quantity of mucus. In the seeds of the almond, the mucus is mixed with oil; but bitter and sweet almonds, under the microscope, exhibit no essential difference.

Modern chemistry, in consequence of the labours of Liebig and Mulder, divided the forms of mucus into three principal groups: into Albumen (vegetable albumen), Fibrin (gluten of the Cerealia), and Casein (legumin of peas and beans), and which are regarded as identical with the substances of the same name found in the animal kingdom. Dumas regards as a fourth group Gelatin (gelatina animalis), which should be regarded as a part of the composition of gluten. Mulder has pointed out that these compounds have all a common basis (H 31 C 40 N 10 O 12),

* Protoplasma of Mulder and others.—Trans.

which he calls Protein; and that the combination of this substance with sulphur (10 Pr + S) forms Casein; with phosphorus and sulphur (10 Pr + 1 P + 1 S), Fibrin; and with more sulphur (10 Pr + 1 P + 2 S), Albumen. There is no means of distinguishing these substances in the cells of plants; and they are all so variable in their peculiarities, that they can only be regarded as groups of substances. Through Liebig's observation*, that these substances cannot be formed in the animal body, but must be taken into it from without, they have obtained a new and peculiar importance. According to the researches of Rochleder and Hruschauer (Liebig's Ann. vol. xlv. p. 253., and vol. xlvi. p. 348.), these substances, when pure, have the power of acting as weak acids. Very important in this relation is their constant union with alkalies and earths, especially the phosphatic salts (perhaps double salts) in the vegetable and animal organism.

§ 11. The substances mentioned in § 9. constantly pass from one into the other, and the presence of mucus in the cells appears necessary for this object. They appear to go through, successively, all the forms from sugar, the most soluble, to cellulose, the most insoluble.

From the preceding remarks it will be seen, that the substances mentioned in § 9. are not so well defined forms of matter as sulphuric and sulphurous acids, or as the protoxide and peroxide of iron, but that a pretty constant series of changes occur in the passing of one substance into the other. Artificially we may produce this series of bodies by mixing them with mucus, or acting upon them with sulphuric acid or alkalies, or even by slighter chemical processes, as repeated solutions and evaporations. The property possessed by mucus, sulphuric acid, &c., of producing chemical changes without themselves becoming changed, has been called by Berzelius catalysis, by Mitscherlich the action of contact (Contactwirkung), and by Liebig by another name, but without any explanation. In the first place, we ought to satisfy ourselves that it is so. In those plants where the first-named bodies are in contact with mucus, a constant metamorphosis seems to be going on, and only rests for a short time at one point. Almost all these changeable bodies are compounded according to the same chemical formula, and vary sometimes in the quantity of oxygen, but mostly in the quantity of water, they contain. Does it not appear very probable that they possess a common basal principle, and that, through varying proportions of water, and through physical conditions, as cohesion, &c., they assume so many appearances? It appears to me that there is here a great field for chemical inquiry.

The mysterious property of the physical processes which is called life, and which is supposed to depend on an especial vital principle, has been made use of from the fact of certain chemical actions and re-actions going on which have escaped observation, but which all allow to go on in the commencing combinations. We know now with certainty, because these changes go on out of the plant, the transition of cellulose into starch, of starch into dextrin, of dextrin and cane sugar into grape sugar, and of grape sugar into gum (as in the fermentation of beet-root juice). All these metamorphoses, with the exception of the first, which is effected only through sulphuric acid, can be produced by the agency of nitrogenous substances (mucus). With great probability it may be con-

* This is not Liebig's, but Mulder's, observation. — Trans.

cluded, from observations on substitution in plants, and supported by chemical analogy, that there is a transition from sugar into dextrin, from dextrin into starch, amyloid, cellulose, and vegetable jelly, from wax into sugar, from sugar and starch into wax, from starch into fixed oils, and from the fixed oils into sugar and dextrin. In these changes the same or very similar compound bodies, through merely taking up or depositing water or oxygen, constitute the very foundations of vegetable change, the formation and metamorphosis of the elementary organs, and thus form an essential part of the so-called life. Any one who would wish to study vegetable physiology, and every botanist must do this who attaches importance to science, will not neglect a thorough investigation of the subjects embraced in the sections of this work concerning Organic Chemistry.

## SECTION II.

### ON THE REMAINING ORGANIC SUBSTANCES FORMED UNDER THE INFLUENCE OF VEGETATION.

§ 12. Amongst the numerous principles present in plants are some which appear to stand in a close relation with the general process of vegetation, and which are generally present: these are, 1. Chlorophyll; 2. the other colouring matters of plants; 3. Malic, Citric, and Tartaric Acids; 4. Alkaloids; 5. Tannin; 6. Viscin and Caoutchouc; 7. Humus.

1. *Chlorophyll* (Blatt-grün, *fæcula viridis*, Chromule, Phytochlor, green vegetable wax). If any green part of a plant is bruised and submitted to the action of alcohol, a green tincture is formed. If this be evaporated to dryness under the exhausted receiver of an air-pump, a green fatty mass is left, which forms soaps with the alkalies. If this is dissolved in ether and mixed with water, and the ether evaporated, small greasy globules are obtained, which appear of a green colour by reflected light, and of a Burgundy-red by transmitted light. Similar globules are separated from the alcoholic solution by a freezing temperature. If the alcoholic tincture is mixed with water and the alcohol evaporated by heat, a part of the fatty substance is thrown down, the water itself is coloured of a brown-yellow, and has a characteristic smell like that of black tea. This is what is commonly called chlorophyll. When treated with sulphuric acid it is either not changed or becomes carbonised; it is not dissolved or coloured blue, as is erroneously stated by Marquart.* It is soluble in volatile and fixed oils.

This substance is found in all plants growing in the light, with the exception of some of the algæ, fungi, and lichens, and the true parasites, covering either conformably the cell-walls or the spiral bands, as in *Spirogyra*, or the granular contents of the cells which are composed of starch or the other similar bodies.† Only in the last sense can we speak of granules of chlorophyll, as granules consisting entirely of chlorophyll are unknown. It is never found in the form of vesicles.‡

* See Hugo Mohl on the Winter Colouring of Leaves, Tübingen, 1837.

† Hugo, Researches upon the Anatomical Relations of Chlorophyll. Tübingen, 1837.

‡ Smith (Elem. Phil. Bot. ed. 2.) does not state how he satisfied himself of chlorophyll vesicles.

Chlorophyll is composed of a white wax-like substance (§ 9.), and a peculiar green colouring matter. Of the first substance it contains more if the first removal of the green parts is effected by ether. The fine green colouring matter originates almost universally under the immediate action of light, which presupposes that there must be universally diffused amongst plants some substance—a colourless chlorophyll, the first form of the pure colouring matter, and which is easily decomposed under the influence of light. To the products of this decomposition belong especially a yellow, a blue, and a blackish colouring matter; and under some circumstances, according to Mulder, wax (?) also appears. The yellow leaves in autumn contain proportionately more wax than the green leaves of summer, the rind of the yellow ripe fruits more than the green rinds of unripe fruits; but in both, starch, or its equivalent, inulin, is found more abundantly earlier than later. The only analysis of this substance hitherto made is the unsatisfactory one of Mulder, $C\,18\ H\,9\ N\,2\ O\,8$, which makes it a nitrogenous body, and which could not be formed out of starch alone. Meyen's defence of this view (Physiologie, bd. i. p. 193.) is a mere fiction. On the other hand, we know that, simultaneously with the origin of every plant-cell, protein and protein-compounds appear, and that these substances, at least, never fail to be present in the parts of plants about to become green. It seems, therefore, more reasonable to look for the origin of chlorophyll from protein. Chlorophyll also appears very closely related with the colouring matter of indigo found in the green leaves of the species of *Indigofera*, of *Polygonum tinctorium*, the *Isatis tinctoria*, &c. The formula of blue indigo is $C\,16\ H\,5\ N\,2\ O\,2$; of white (deoxidized) indigo, $C\,16\ H\,6\ N\,2\ O\,2$. Pure chlorophyll is soluble in hydrochloric acid, sulphuric acid, and the alkalies, with a green colour; it is soluble in ether and alcohol, but insoluble in water. Exposed to the action of light, or treated with hydrogen in *statu nascenti*, it is decolorised.

The various shades of green of the organs of plants depend upon very different causes: partly upon the nature of the chlorophyll, whether it is pure or more or less mixed with the yellow, blue, and black products of its decomposition; partly upon the quantity of chlorophyll in individual cells; partly on the thicker or looser arrangement of these cells, which is evident on the under sides of leaves, which are always of a fainter and lighter green, depending on the intercellular spaces which are there present, and which, reflecting the light white, mixes with and diminishes the intensity of the green. Variegated leaves are produced in one of two ways. First, the single groups of cells contain only the yellow product of the decomposition of the chlorophyll, as in the *Phalaris arundinacea picta*, a variety which appears on a dry soil, but disappears on a moist one; or in the variegated varieties of the common holly (*Ilex Aquifolium*). Secondly, the epidermis separates itself from the cells lying under it in particular places; and the layer of air lying between them appears as a bright silvery spot, as in *Begonia argyrostigma*, *Silybum marianum*, and other plants. In the last place, the green colour of plants may be yet considerably modified through the greater or less secretion of wax upon the surface, which in some cases forms a layer of small silvery scales, which appear almost snow-white, as in *Elymus arenarius*.

2. *Vegetable Colours.* Of these we know at present very little. They may be generally divided into soluble and insoluble. The last are found in the cells of plants in the form of globules of a yellow (*Fritillaria imperialis*), red, and seldom of a blue colour (*Strelitzia farinosa*); they

are frequently soluble in ether, alcohol, volatile oils, and separated from ether in a resinous, not in a fatty, form. The first, as far as I know, are only of a red and blue colour; the red caused by an acid, the blue by an alkali; and are dissolved in the fluid contents of the cell. They may be found in the red parts of plants, and in the flowers of *Echium vulgare.* They all contain nitrogen.* But there are other colouring matters present in plants, as the red in *Iberis umbellata,* and the blue in violets, which become green through the action of alkalies, and which are very different from the foregoing. Chemistry has much to do in this department of inquiry.

A theory was proposed in 1834, by Clamor Marquart, in a book on the colours of plants, which supposed that two modifications of chlorophyll, *Anthoxanthin* and *Anthocyan,* the one containing a little more, and the other a little less, water than chlorophyll, were the cause of the red and yellow series of colours, and chlorophyll of the blue. Although this theory is adopted by Endlicher and Unger, in their "Rudiments of Botany," it is not founded on sufficiently accurate data to demand refutation. Berzelius (Handbuch der Chemie) and Mulder (Physiol. Chem.) have both written on Chlorophyll, and I have mostly followed the latter in the foregoing remarks. The remaining colouring matters important in the arts, but unimportant physiologically, demand attention.

3. *Tartaric Acid* (*Acidum tartaricum,* $\bar{T}$.), *Citric Acid* (*Acidum citricum,* $\bar{C}$i.), and *Malic Acid* (*Acidum malicum,* $\bar{M}$a.), are either found together or alone in all sour fruits, and perhaps also in all acidulous juices of plants, for malate of lime is found in the *Sempervivum tectorum.* From the process of ripening in fruits, it has been concluded that these acids stand in a peculiar relation to sugar; that they are easily formed out of it, and as easily pass into it. Liebig (Organic Chemistry) has gone so far as to presume that, in the presence of alkalies, carbonic acid and water are converted into hydrated oxalic acid, and this into tartaric acid, malic acid, and, lastly, this into sugar and dextrin; and that thus the organic acids stand in a middle place between the organic and inorganic bodies. This is one of Liebig's most genial combinations, but has no observation on which to rest. The chemical composition of these acids, according to Berzelius and Liebig, is as follows: —

| | C | H | O |
|---|---|---|---|
| Tartaric Acid - - - | 8 | 4 | 10 |
| Citric Acid - - - - | 12 | 4 | 12 |
| Malic Acid - - - - | 8 | 4 | 8 |

4. *The Alkaloids,* like the acids, are, as far as we know at present, only so far important as the remarks of Liebig (Organic Chemistry), on both classes of substances, extend. Many plants appear to have a facility, when it is necessary to neutralise a base by an inorganic acid, or an acid by an inorganic base, and these substances fail, of substituting for them organic acids and bases. Thus we find that potatoes sprouting away from the soil form Solanin; thus Quinine, Cinchonine, and Lime, take the place of each other in the Cinchona barks, and Meconic acid is found in opium to take the place of Sulphuric acid.

5. *Tannin* (Tannic Acid). In most plants, and especially the Phanerogamia and Ferns, there is frequently found a substance which reddens litmus, tastes astringent, and changes animal gelatine into leather. This substance appears to be modified in different plants. It is found

* According to Liebig, Organic Chemistry.

more constantly in cells presenting a low degree of vital activity, as those of the wood and bark; and those of early decaying excrescences, as galls: but still it is found in many leaves, as those of the tea-plant, and of the *Ericaceæ;* but here, perhaps, it only occurs in the bundles of vessels, or less actively vital cells, of the leaf. Frequently the cells of the bark have few or no contents; and I may, perhaps, hazard the opinion that the tannin is only found in the cell-wall, and perhaps as a product of the commencing decomposition of the cellulose. If two equivalents of cellulose, C 24 H 20 O 20, take up 16 O from the air, and 12 HO (water), and 6 $CO^2$ (carbonic acid) disappears, there will be left one atom of tannin (C 18 H 8 O 12). The formation of tannin may be conveniently regarded as the commencing process of putrefaction in the cell-membrane. According to Mulder's formula of cellulose, C 24 H 21 O 21, only 4 O would be taken up; and by the disappearance of 13 HO, an equivalent of tannin would be formed. In the living cells of plants, many substances are found which cannot exist with tannin, such as mucus* (Schleim).

6. *Viscin* (Birdlime), and *Caoutchouc*, have not been, up to this time, sought after and examined, except in a few plants. Viscin is a clear, very gelatinous, substance, and insoluble in water; it is found in the berries of the mistletoe (*Viscum album*), in the fruits of *Atractylis gummifera*, and in the milky juice of the green twigs of *Ficus elastica.* Under this head we must also include the peculiar substance found in the proscolla of the *Orchideæ*, and which exists as a fibrous tissue between the pollen grains in the same plants; likewise the fluid which exudes from the glands on the stigma of the *Asclepiadeæ;* and, lastly, the product of the glands under the anthers of some *Apocyneæ*, as in *Nerium Oleander.* If the history of the development of these parts is examined, as well as the formation of the viscin in *Viscum album,* it will be found that this substance is formed through the solution of existing cells. It is well known, that in nearly all decompositions of cellulose, carbon remains in excess; and this agrees with the composition of viscin, which contains, according to Macaire Prinsep, C 75·6 H 9·2 O 15·2.

Caoutchouc, or at least an essential element of it, appears to stand in the same relation to viscin as gum to pectin. It belongs to the excretory substances, and is found in the milky juice of plants, especially in the three Jussieuean families, *Urticeæ*, *Euphorbiaceæ*, and *Apocyneæ.* The milky juices of other plants are comparatively poor in this substance, although it is absent in none of them. This substance, which defies all chemical agents, swells up and diffuses itself (not dissolves) in ether, and on dry distillation renders some remarkable chemical products (see Himly de Kaoutschouk ejusque siccæ Destillationis Productis; Göttingen, 1835); has many peculiarities and unexplained properties; and its relation to plants, its origin, &c., are at present almost entirely unknown. In the milky juice of plants, it is found diffused emulsively in the form of little globules. If the juice be allowed to stand, especially if diluted with a little salt water, it collects on the surface in the form of a white cream, which, when dried, is of a yellowish colour, and almost perfectly transparent. Schulze, who, in all his views on milky juice and milk-vessels, is dreamy, regards Caoutchouc as analogous to the fibrin of blood. Any one who examines the milky juice of *Siphonia elastica*,

* Endlicher and Unger say that the tannin is always dissolved in the cell-juice. How comes it, then, that perfectly juiceless oak bark contains so much tannic acid?

and still holds by Schulze's opinion, either cannot or will not see. I can confirm all that Berzelius has said on this subject in his Chemistry.*

7. *Humus* (Humin, Humic Acid, Ulmin, Ulmic Acid, &c.). If dead animal and vegetable matters are exposed to the action of moisture and the atmosphere, oxygen from the air is absorbed; the nitrogen unites with hydrogen to form ammonia, which, either alone or in combination with carbonic acid formed at the same time, disappears if it be not fixed by some acid previously present or formed at the same time. The carbon forms carbonic acid; the hydrogen, combining with the oxygen of the air, forms water, and with its nitrogen, if the decomposition takes place in a closed vessel, or as it does in the soil, forms ammonia; at last nothing remains but the inorganic salts of the plant or animal. Between these changes, however, a number of other substances occur. The indifferent, insoluble, richly carbonaceous mass, when it is black, is called Humin; when brown, Ulmin. Further, from these five acids present themselves, humic, ulmic, geinic, crenic, and apocrenic acids. They were long regarded as substances between resin and wax, and can be obtained in considerable quantities from vegetable mould composed of leaves six years old, by washing with ether. The acids combine with the alkalies, and even with the earths, and form soluble salts which constitute the so-called humus-extract. The mixture of these substances, combined with portions of the rocks which form the surface of the earth, constitute the arable land or cultivable soil, and which is the natural and most promising medium of growth for the greater proportion of plants. The first-formed in time is the ulmic acid, which consists of C 40 H 14 O 12. This, through absorption of 2 O, and the separation of 2 H O, is converted into humic acid, C 40 H 12 O 12; and this, through the absorption of 91 O, and the separation of 40 $CO^2$ and 24 H O, is changed into geinic acid, C 40 H 12 O 14. These three acids are almost insoluble in water, and are precipitated by strong acids from alkaline humus-extract. There remains in the solution crenic acid (C 24 H 12 O 16), and apocrenic acid (C 48 H 12 O 24): the last through acetate of copper, and the first through acetate of copper and carbonate of ammonia, are precipitated as crenate and apocrenate of copper. The following may be taken as an example of the formation of these substances:

| | | | C | H | O | N |
|---|---|---|---|---|---|---|
| 7 Eq. | of Cellulose + 80 | = | 84 | 70 | 78 | 0 |
| 2 Eq. | Humin | = | 80 | 24 | 24 | 0 |
| 4 | Carbonic acid | = | 4 | 0 | 8 | 0 |
| 46 | Water | = | 0 | 46 | 46 | 0 |
| | | | 84 | 70 | 78 | 0 |
| 1 Eq. | Protein + 4 Eq. O. | = | 40 | 31 | 16 | 10 |
| 1 Eq. | Humin | = | 40 | 15 | 15 | 0 |
| 1 | Water | | 0 | 1 | 1 | 0 |
| 5 | Ammonia | | 0 | 15 | 0 | 10 |
| | | | 40 | 31 | 16 | 10 |

For further information on these substances, the reader may consult Mulder, Bulletin des Sciences Phys. et Nat. en Néerlande Année, 1840, liv. i., and Physiological Chemistry.

* Gutta Percha belongs to this group of vegetable products. — Trans.

§ 13. Besides the substances mentioned in the foregoing paragraphs, there are a countless mass, the smaller part of which only are probably at present known, and which appear generally to exert but a very small influence upon the life of the plant. To these belong the substances called by chemists Alkaloids and Vegetable Acids, Resins, Essential Oils, Colouring Matters, &c. Many of these must be regarded as mere secretions, and this would not be the place even to recount them. They may be sought for in manuals of Chemistry.

A great part of the vegetable acids, almost all the alkaloids, and many of the resins, are found in cavities (*receptacula*), or in the so-called latex-vessels, but never in the plant-cells. Others, as the essential oils and resins, are found in solitary cells, which they exclusively fill, and in which it is impossible for any chemical change to take place, so that the cell appears dead. Many amongst them, under peculiar circumstances, fail to be developed, as the poisonous secretion of hemlock, which is not found in the plant of the Asiatic steppes; whilst others are substituted, the one for the other, without the vegetation of the plant suffering in the smallest degree. Therefore, in the contemplation of the phenomena of vegetable life, I think they may, in a great measure, be disregarded as unimportant substances. Upon these bodies, then, I have little or nothing to say, and especially as chemistry has scarcely begun to work upon them.

# SECOND BOOK.

# ON THE PLANT-CELL.

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## CHAPTER I.

### FORM OF THE PLANT-CELL.

### SECTION I.

#### THE CELL REGARDED AS AN INDIVIDUAL.

§ 14. ONLY in a fluid (*cytoblastema*) containing sugar, dextrin, and mucus (protein), can cells be formed. This is effected in two ways: 1st. The particles of the mucus are drawn together into a more or less rounded body, a cell-kernel (*cytoblastus*), and change the entire surface of one part of the fluid into jelly, a relatively insoluble substance. Thus originates a closed gelatinous vesicle, into which penetrates the external fluid, and distends it, so that the mucus-corpuscle on one side is free, and on the other remains adherent to the inner wall of the vesicle or cell. It forms then a new layer on its free side, and is thus enclosed in a duplicature of the wall; or it remains free, and is then mostly dissolved and disappears. During the gradual extension of the vesicle the jelly of the wall is commonly converted into cellulose, and the formation of the cell is completed. 2d. The collective contents of a cell are divided into two or more parts, and around each part there is immediately formed a tender gelatinous membrane. In this way many cells are formed, which fill up the cell in which they originated.

Of the nature of the fluid in and out of which the cells originate, we are not yet perfectly cognisant. Thus much we know, that in some cases (in the embryo-sac of the *Leguminosæ*, for instance) a solution of sugar is present; and, as far as may be decided by the action of alcohol, this is mixed with gum (dextrin ?). The constant presence of a nitrogenous substance is also necessary, and which we should have anticipated from previous considerations (§ 11.).

In all tender hairs, almost in every growing portion of cellular tissue,

and especially striking in some monocotyledonous orders, as *Orchideæ*, *Commelineæ*, and *Asphodeleæ*, also in many dicotyledonous orders, as the *Cacteæ*, *Balanophoreæ*, &c., in the entire leaves of Mosses, especially in *Sphagnum*, we find in every cell, fastened to the inner wall, a small, mostly plano-convex or lenticular, sharply defined body, strikingly different from all other contents of the cell. This is the cytoblast. It is met with in all newly-formed cellular tissue, but later it disappears from the same cells. It is seen in various stages of perfection. When perfectly formed, it is a flat, lenticular, sharply defined, transparent, pale-yellow body, in which it is easy to distinguish one or two, seldom three, sharply defined and evidently hollow corpuscles, which are called *nucleoli*. In its most imperfect form it appears merely as a flat, yellow, semi-granular globule, in which there are no nucleoli, and which do not appear later. It varies much in its character, according to the plant as well as its age: in colour, from perfect clearness to a dark yellow grey; by iodine it is converted from a pale yellow to a dark brown: in consistence, from a granular mucilage to a firm homogeneous mass: in the number of its nucleoli, from one to three; in the form of the same, from an entire absence through a simple globule to one that is hollow: in its own form, from the globular to the lenticular and to the egg-formed disc: in its absolute size, from 0·00009 to 0·0022 of an inch in circumference: in its relative size, from the cells which it fills to those in which it forms, not more than the five-hundredth part of the inner surface of the cell-wall; and lastly, in its attachment to the cell-wall, from a loose adhesion to a perfect union with the cell-wall and enclosure in a duplicature of the same. With the exception of the nucleoli, the first statements relate universally to the younger states of the cytoblast.

In those cases in which I have been able to observe completely the origin of the cytoblasts, as in the albumen (perisperm) of *Chamædorea Schiedeana*, *Phormium tenax*, *Colchicum autumnale*, *Pimelea drupacea*, and many papilionaceous plants, I have found that they appear at first amongst the little mucus-granules of the formative fluid, and that they are gradually accumulated around the nucleoli; and as they combine together to a greater or less degree, a thicker or thinner disc is formed, and sometimes two or three such discs lie near one another, and at last the cytoblast presents itself. All this takes place before a cell can be seen.* In young cells I frequently found the cytoblast convex, granular, yellow, with the nucleoli simple: in older cells of the same plant, flat, homogeneous, uncoloured, the nucleoli hollow (e. g. *Cacteæ*).

In the *Cryptogamia* the cytoblasts are not so generally seen, yet they are present in the spores of Ferns, Mosses, Lichens, and some Fungi, and now and then in the cellular tissue of Algæ, and in the cells of *Spirogyra*, free in the midst of the cell.

A chemical analysis of the nucleoli is at present impracticable.

That the cytoblast is a nitrogenous body, a protein-compound, and perhaps in its simplest state pure protein, is proved by its colour, consistence, behaviour towards iodine, alcohol, alkalies and acids, and concentrated nitric acid; and by the researches of Payen, confirmed by Mulder, on the protein-compounds in the spongioles and in the cambium, compared with the microscopic analysis of those parts.

Thus far extend my own observations, but recently Nägeli has considerably enlarged them. (Schleiden and Nägeli, Zeitschrift für Wis-

* See Plate I. fig. 1. *a*, *b*; 3.; 4. *a*, *b*; 5., with the explanation.

sentschaftliche Botanik.) He has proved the existence of the cytoblast in all the families of the *Cryptogamia*, especially the *Algæ*, and shown that it is necessary to distinguish between a parietal and central nucleus.* The central nucleus subsequently becomes hollow, and may be increased by division. I cannot, however, agree with Nägeli when he asserts that the cytoblast consists of an external membrane, with contents. I regard this as a later stage of their development, for in the young free cytoblasts there is no trace of a distinct membrane, and the origin of the free cytoblast forbids such a supposition. Observation, however, on this subject is not yet brought to a close ; and many things will occur to modify, extend and explain our present knowledge.

*Complete Observations upon the Formation of Cells.* — I. When the cytoblasts are perfectly formed, they soon present a delicate membrane, which encloses them, and which is sometimes extremely fine and soft, and sometimes thicker and more compact. † This membrane soon becomes elevated on one surface of the cytoblast in a vesicular form, and gradually extends itself, so that the cytoblast occupies at last only a small part of the wall ‡; but still the cytoblast continues to enlarge, and the nucleoli become more evidently defined. The membrane of the vesicle, or young cell, becomes gradually stronger and thicker ; it gets a round, or sometimes an elongated, form, and sometimes an irregular edge, which subsequently disappears.

In the youngest state of the cell the cytoblast is generally covered on all sides by a delicate membrane, which is not coloured by iodine. Mohl (Botan. Zeitung, 1844) has clearly not understood my observations in the paper which I published in Müller's Archiv for 1838, and in which I first made known my discoveries on this subject. As soon as this primary cell membrane is removed by extension, at some distance from the cyloblast, it is often found covered with a delicate layer of semifluid mucus, which is sometimes seen circulating in little anastomosing streams, sometimes granular, sometimes entirely homogeneous and clear, and which when present may be made visible by the action of nitric acid, alcohol, and iodine. This is Mohl's primordial utricle. It is directly on the boundary between the membrane and its contents, that the most active chemical processes take place ; and this goes on as long as the necessary conditions are present, especially the formation of nitrogenous matters. It is, therefore, not improbable that this layer is the agent in converting the newly introduced constituents of the cell into cellulose, and thus of thickening its walls (or even forming new cells). But at last these protein-layers are dissolved and decomposed, and disappear. In old cells, especially of wood, no trace of these layers is found, and generally only a small quantity of nitrogenous matter at all. I can understand how it is that Mohl may doubt the existence of a membrane free from nitrogen, for I am far from asserting that my observations are complete; but I am at a loss to explain how Unger can affirm that the cytoblast is first formed after the development of the cell-membrane. (Linnæa, vol. xv. part ii. 1841.) I have just been examining (June, 1845) the spongioles of *Cypripedium Calceolus* and *Neottia Nidus avis ;* and although at first I was doubtful as to whether any thing existed besides the great cytoblast, yet, when I employed nitric acid and iodine, I found surrounding the cytoblasts cells which required a longer period for development in

* See Nägeli on the Formation of Cells, translated by A. Henfrey for the Ray Society. 1845.—Trans.

† See Plate I. figs. 1. *c*, 4. *c*.

‡ See Plate I. figs. 1. *d*, 2. 14, 15, 16.

the mother cells, and which last subsequently disappeared first. I find it, in fact, impossible to obtain such a section as is represented by Unger (table v. op. cit.).

There often appears on the free side of the cytoblast, as, for instance, in the *Fritillaria imperialis* and in *Chamædorea Schiedeana*, a new lamella, which, at the edge where it touches the cytoblast, combines with the first cell wall, and thus encloses the cytoblast. Such cytoblasts seldom undergo any further change. The cytoblast, after the formation of the cell, sometimes becomes absorbed, and sometimes remains for the entire life-time of the cell. The cell at first consists of jelly (gallerte), and easily dissolves in water; gradually it becomes changed into cellulose. I have traced accurately the steps of this change in the albumen of *Leucojum æstivum*, *Phormium tenax*, *Colchicum autumnale*, *Chamædorea Schiedeana*, *Pedicularis palustris*, *Momordica Elaterium*; in *Lupinus*, and many other *Leguminosæ*; in the embryo sac of *Alisma Plantago*, *Sagittaria sagittæfolia*, *Pedicularis palustris*, *Œnothera crassipes*, *Tetragonia expansa*; in the germinating cotyledons of *Lupinus tomentosus*; in the many-celled hairs of *Solanum tuberosum*, and many other plants; in the sporangia of *Borrera ciliaris*; and in the sporocarpium of *Blechnum gracile*.

II. In addition to the above mode of cell-formation, Nägeli has described a second, which he first observed in the formation of the primitive cells of the pollen, and has more recently found to exist in a large number of *Algæ*. Mohl imagines something of the same kind to take place in the new cells of the cambium. To this mode of cell-formation belong all those cases where the division of cells takes place. I have not had an opportunity of making any observations on this subject, but the following facts are after Nägeli: — So long as a cell is internally covered with a layer of mucus, this process may go on. In the first place, this mucus layer is divided into two or four parts, each of which is surrounded by a delicate layer of mucus. These external mucus layers are converted into cellulose, and thus two or four little sacs or cells are formed, which perfectly fill up the primitive cell. In a peculiar and hitherto unexplained way, the cytoblast seems to be very active in this process. This increase takes place in most instances in cells with a central cytoblast, and this divides itself into two or four cytoblasts, each of which becomes the central point of a new cell. — No objection can be made to this history of cell-formation founded upon such careful observations. Of the part it plays in the vegetable kingdom Nägeli has given the following account. It seems to be the only mode of cell-formation in the *Diatomaceæ*, *Nostochineæ*, *Oscillatorieæ*, *Batrachospermeæ*, and *Fucaceæ*. In the *Confervæ* it takes place in all the cells except those of the spores. It also takes place in the special mother-cells of the tetrasporous plants, as the *Florideæ*, *Hepaticæ*, frondose Mosses, Ferns, *Lycopodiaceæ*, and *Phanerogamia*. In the *Fungi* and Lichens, in the *Ulvaceæ*, and in the formation of the spores of *Characeæ* and *Equisetaceæ*, it is at present unknown. On the other hand, with the exception of the special mother-cells, it is not found in the cells of the *Characeæ*, *Equisetaceæ*, *Florideæ*, *Hepaticæ*, frondose Mosses, Ferns, *Lycopodiaceæ*, and *Phanerogamia*, in all of which the cell-formation takes place around a central nucleus. Probably, further observations would bring this process under the same general law as the preceding.

*Imperfect Observations.*—There are some cases where the cells are very small and delicate, and nearly filled with granular contents, and where a

part of their layer obscures observation, and where from other causes it has been found impossible to make complete observations. Nevertheless, I have seen very generally, especially after the use of nitric acid, by which the cells are separated from one another, sometimes two cells, with their cytoblasts in a single cell in *Gasteria nitida*, and in the terminal buds of *Cypripedium Calceolus*, and in the spongioles of the last plant, and of *Neottia Nidus avis* two cytoblasts loose in a single cell, and near by two cells with cytoblasts enclosed in another cell. All young cellular tissue in the *Phanerogamia*, without exception, exhibits the cytoblast. In the development of the pollen, the cells are seen filled with a thick grumous fluid, which separates into four parts, around each of which there is suddenly developed a tolerably thick membrane. These might be regarded as four large cytoblasts, if the appearance of the membrane was not attended with another characteristic cytoblast. But I have observed in *Passiflora Princeps* and *Cucurbita Pepo*, at the time when the dark mass in the primitive cell was yet undivided, a number of clear cells, each with a little clear cytoblast enveloped in this dark mass. May not these be the pollen cells, which gradually form within, take up the grumous matter, and, again precipitating it gradually in their cavity, grow thereby, and, suddenly dividing into four parts, become visible? I have not made any observations on the intermediate stages, and Nägeli (in the paper before quoted) thinks he has observed another process. I have, however, found some interesting facts in *Rhipsalis salicornioides*, which I have not had an opportunity to follow up.

*Inferences from the above Facts.*—Up to the present time no fact has occurred which is not in accordance with the complete precedence of the cytoblast, as above observed. The indications of its precedence are only obscure and incomplete in those cases in which accurate observation is surrounded by insurmountable obstacles. It is in the formation of the spores, the foundation of the future plant, in *Cryptogamia;* in the embryo, the young plant itself, of the *Phanerogamia*, that the precedence of the cytoblast is fully made out. Both serve as points of support for analogous conclusions in other cases; and it appears, until further researches may necessitate modification, that we may safely conclude that the precedence of the cytoblast in the formation of cells is a universal fact.

If, further, we regard the easy transformation of the assimilated matters, and may from artificially conducted experiments draw the conclusion that the nitrogenous matter which I have called mucus, and which forms the cytoblast, is the substance which calls forth these transformations, and if we further remark that sugar and dextrin are more easily soluble than jelly, and that sugar and gum are changed into jelly if the quantity of water is not increased, and which must be necessarily precipitated, we must regard the whole process of cell-formation as simply a chemical act. The gathering together of granules of mucus to form the cytoblast we can as little explain as that, when we form a solution of two salts, if we throw into the mixture a crystal of one or the other salt, that salt alone crystallises around it.

*Analogies.*—Schwann has pointed out, in an acute and profound treatise*, that the animal organism also is composed of cells, and that

* Microscopic Researches on the Analogy in the Structure and Growth of Animals and Plants. Berlin, 1839. Although in this work the analogies between the formation of vegetable and animal tissues are pointed out, it should be borne in mind that there are some tissues which are peculiarly animal, and which constitute the distinction between the plant and animal. Some of the animal tissues, such as the cell and nucleus

these cells are formed in the same way as those of plants. If this law is found essential to some plants and animals, this analogy forms a basis for enunciating this mode of formation as a universal law for both kingdoms of nature.

In the same work Schwann has given an interesting comparison between the formation of crystals and cells, and he was led to this from a consideration of the nature of the substances of which the last are formed. This view in future may be of the greatest importance, as it shows that the apparent gulph between the organic and inorganic kingdoms may not be impassable. There is one point to which I would allude, and which seems to have escaped the attention of Schwann. In the formation of the crystal, the matter of the same already exists, as such, dissolved in the fluid, and only awaits the withdrawal of the solvent to assume its peculiar form: it is otherwise in the cell of the plant. Here the organic substance forming the substance of the cell is not present in the cytoblast, but is formed through another necessarily present substance, and this only takes place when the new-formed substance is relatively insoluble.

In the crystallisation of salts, such as the nitrate of potassa, from a solution, we can observe the increase of the crystal from additions to it from without. But, on the other hand, if we take a solution of two substances which form, when mixed, a precipitate, we shall find, on examining this under the microscope, that a membrane divides the two fluids. Accurate observation will show that this membrane consists of crystals of various sizes. If the fluid remains quiet, some of the crystals are projected into it on both sides; if the fluids are mixed, the crystals are dissolved up again. After many careful observations, I believe that all inorganic substances, if they are allowed to remain quiet, assume a crystalline form; and that the so-called pulverulent precipitates consist of crystals, the form of which, from their smallness, cannot be observed.

In the last place I must mention a highly interesting analogy, which, when more accurately examined, may perhaps one day lead to the most satisfactory explanation of the process of cell-formation,—I mean vinous fermentation. We have here a fluid in which sugar and dextrin, and a nitrogenous matter, as a cytoblast, are present. At a certain temperature, which is perhaps necessary to the chemical activity of the mucus, there originates, without, as it appears, the influence of a living plant, a process of cell-formation (the origin of the so-called fermentation-fungus), and it appears that it is only the vegetation of these cells which produces the peculiar changes that occur in the fluid. Whether this organism is really a fungus, is a matter of indifference; but whether it alone, through the activity of its vital processes, determines the process of fermentation, deserves to be accurately determined.

I will here add my own observations on these fermentation-cells. I bruised some currants with sugar, and, having pressed the juice through a cloth, diluted it with water and filtered through folded paper. The fluid was bright red, quite clear and transparent, and, under the microscope, showed no trace of granules, but presented a number of little drops of a pure clear oil. At the end of twenty-four hours the whole fluid was opalescent, and presented, under the microscope, a number of granules suspended in it (fig. 9. *a*, Plate I.). On the second day these granules had greatly increased, and there appeared amongst them perfectly-formed ferment-cells (Plate I. fig. 9. *a*, *b*, *c*). There also appeared, now and then,

fibres (Henle, General Anatomy), have no analogues in plants. [Schwann's treatise has been translated and published by the Sydenham Society.—Trans.]

vesicles of carbonic acid gas. On the fourth day fermentation was very active. At the bottom of the vessel, and on the surface of the fluid, yeast had formed: but these yeasts consisted of single cells, or several attached one to another. In the solitary cells could be observed the way in which one cell was formed from another (Plate I. fig. 9. *d, e, f*). The ferment-cells do not in this state permit of a distinction between the contents and the membrane of the cell. In the midst of the cell there is a transparent spot; but whether hollow, or a solid nucleus, I could not decide. The remaining parts appeared entirely homogeneous, yellowish like a nitrogenous substance, sometimes mixed with small solitary granules (Plate I. fig. 9. *d, e, f*). In a similar way, a solution of sugar with elder-flowers was examined, and gave similar results. Other results were obtained in the following way. Pure white protein (albumen), from the white of an egg, was dried, and rubbed down with sugar, and left to ferment: the fluid at first was perfectly clear. On the third day, the small portions of protein, which at the commencement exhibited a sharply angular aspect, assumed partly a granular aspect, and some a more or less rounded form. These globules showed an active molecular movement, and some appeared strung together. On the fourth day there was seen between these granules round or elongated cells, which were either solitary, or arranged together in a line with a tendency to the formation of branched fibres. These cells were not more than one-third of the diameter of ordinary ferment-cells (Plate I. fig. 10. *c, d*). An active fermentation went on, and gas-bubbles were given out from the protein-granules and the linear cells. Proper ferment-cells did not make their appearance. Fluid albumen, mixed with sugar and filtered, became thickened on the second day, and contained little granules of albumen (coagulated?). The further phenomena were similar to those exhibited by the preceding, except that there were developed a few true ferment-cells. Protein moistened with water displayed the same appearances as when mixed with sugar and water; ultimately putrefaction came on, and the development of infusoria, but the vegetable formation preceded. There appear to be two very different types of ferment-cells, according as the fluid contains organic acids and essential oils or not. From the phenomena exhibited by the ferment-cells, one might be inclined to regard them as similar to animal-cells, which are formed through a cavity in the cytoblast, and which afford indications of the nucleoli in their highest development. But this analogy is not tenable, and the above observations must be regarded as imperfect. If we take fully developed ferment-cells, and treat them with ether, alcohol, or caustic alkalies, there will be found in the fluid a number of globular delicate cells, with thin but clearly distinguishable walls, which contain a clear fluid, with here and there very small granules, which, alone or in groups, are attached to the inner surface of the cell-wall, and (almost?) always a large round flat body (a cytoblast?).

*History and Criticism.*—Before the discovery and scientific use of the microscope, of course there could be no accurate knowledge of the cells of plants.

Robert Hooke, an Englishman, was the first discoverer of the cellular structure of plants. He used a microscope first brought to England by Cornelius Drebbel in 1619. (*Micrographia.* London, 1667. Fol.)

Marcello Malpighi, professor at Bologna, gave a more accurate account of the structure of plants. He sent to the Royal Society of London his great work, Anatome Plantarum, in the year 1670, and which was published in two volumes folio, at the expense of the Society, in 1675 and

1679. This work claims for him the title of the creator of scientific botany. He is so accurate, and pursues so correct a method, that it was a century before the time at which he wrote it, and at the present day many so-called botanists do not know so much of plants as Malpighi. He not only observed the cellular structure of plants, but maintained that it was composed of separate cells, which he called *Utriculi.*

Nehemiah Grew was secretary to the Royal Society at the time Malpighi's work was publishing. He published his Anatomy of Plants in 1682; is much indebted to Malpighi. He first took up the wrong view that the walls of cells are composed of fibres; he also, by comparing the cells of plants to the froth of beer, would appear to have thought that they were mere cavities in a homogeneous substance, a view which was afterwards supported by C. Fr. Wolff in his Theoria Generationis, Halle, 1774. These false views have in modern times found supporters: the first in Meyen, in his Physiology of Plants (vol. i. p. 45.); the second in Mirbel and Unger. Meyen founds his notion of the fibrous structure of the cell-wall on having observed this structure in a new species of orchid from Manilla. This is, however, not a singular appearance, and an inquiry into the history of the development of the cells would have dispelled the delusion.

Mirbel has recently attempted * to support his view of the origin of the cells as mere cavities in a homogeneous saline mass which he calls cambium, by observations on the root of *Phœnix dactylifera.* This paper is very incomplete, and the author has adopted a new system of nomenclature, which makes it difficult to follow him. Thus far I can say, that no such division of continuity filled with a mucilaginous mass (his *cambium globuleux*) between the bark (his *région périphérique*) and the external portion of the woody bundles of the root (his *région intermédiaire*) exists as he describes. I have constantly found present cellular tissue. Nor are the woody bundles of his *région intermédiaire* surrounded by this substance, but by cellular tissue. He is also deceived in the nature of the contents of the cell by their intermixture with water.

Unger (Bot. Zeitung, 1844) has published some observations on the growth of the stem, in which he doubts whether the cytoblast is the origin of the cell. In the instances where he has not observed the cytoblast in the cells they had been evidently absorbed, whilst in those in which he has seen and drawn them he has represented them to meet his own views.

The views of Sprengel on the origin of cells from starch granules, the similar ones of Du Petit Thouars and Raspail, and those of Turpin on the nature of globuline, under which term he includes starch, mucus, colouring matters, &c., do not deserve a scientific refutation. Other observations on the origin of the plant-cell are unknown to me. Most botanists pass the subject over in silence, although there can be no doubt that it forms the introduction to a strictly scientific investigation of vegetable structure.

In conclusion, I refer to Robert Brown (Observations on Orchideæ, Trans. Linn. Soc. 1833), who has here, as in so many other instances, opened up a new path of inquiry. He first observed the cytoblast, as a body, frequently present in plants: he did not, however, know its significance in relation to the life of the cell; he called it "nucleus of the cell."

§ 15. The free independent cells of plants are developed in a globular form. Their subsequent forms appear to depend on the dissimiliar nutrition of individual parts of the cell-wall, and a con-

* "Nouvelles Notes sur le Cambium," read at the Academy of Sciences, April, 1839.

sequent irregular distension. Several forms of this nutrition may be distinguished.

*A. Many-sided, or a nearly uniform, nutrition.*—From this arises globular or elliptic cells; or, if pressed on all sides, polyedral cells; or, in a regular arrangement, dodecaedral cells. When the parts deposited are unconformable, little protuberances projecting on all sides in the form of rays are developed, which constitute stellate cells.

*B. Nutrition in the dimensions of the plane.*—From this arises tabular cells; or, if the nutrition goes on in three dimensions of one side, plano-convex cells; but if the nutrition goes on in one direction of the surface, then long small tabular cells, which may be called strap-shaped. With an irregular extension this form of nutrition developes rayed or stellate cells.

*C. Nutrition in one direction, extension in length only.*—The cells formed are the cylindrical, prismatic, and fibrilliform.

That an irregular nutrition is the principal cause of the variety in the forms of cells is in the highest degree probable. Cells which are not immediately in contact can only be nourished in those spots where they are in contact with other cells; and cell-walls in contact with air do not continue to grow in that direction, but become flattened, as in the upper surface of epidermis cells, and in the cells of the partition-walls of air-passages on both sides. In the air-passages, when young, there are globular cells which touch only at particular points: from the rapidity with which the sap passes through these spaces, and is decomposed by the air, these cells are only nourished at the points where they touch, and the points of contact continue to grow, so as to form rays which constitute the stellate cells of the partition walls, and the spongiform cells of the air-passages. This irregular nutrition may also take place in cells with perfect contact: in these cases the projecting rays are disposed alternately, as is the case in many epidermis cells, whose edges appear waved or toothed on the surface.

But the most decided proof that irregular nutrition of the cell-wall is the cause of the various forms of cells, has been afforded by Nägeli*, in his researches upon *Caulerpa prolifera.* It consists of a little creeping stem with roots below and leaves above, and sometimes forming branches on the sides, and originates in the growth of a body which may be regarded as an individual cell. The large size of the parts admit of an easy distinction being made between the old and young cells, as well as the origin of the various forms from the differing nutrition of the individual parts of the cell. The diversity of growth in individual cells admits of analogy between the morphological distinction of stem and leaf in the higher plants, as between the leaf and stem divisions of the single cell in the present case.

All the various forms of cells, with the exception of the globular, elliptic, and fibrilliform, originate in the combination of many cells with one another. Every free cell forms for itself an arched surface; polyedral cells originate from the mutual pressure of cells. If perfectly formed cells of the same size are allowed to press against each other, they will form rhombododecaedrons. The rhombododecaedron, although frequently present, must not be regarded as the primitive form of the cell.

* Schleiden and Nägeli, Zeitschrift für wissentschaftliche Botanik, part i. p. 134—165.

*History and Criticism.*—It is usual to distinguish a number of elementary organs in plants, and, although mostly regarded as forms of the cell, yet Link and Treviranus adhere to three, the cell, the vessel, and the fibre. It is, to say the least of it, unphilosophical to assume that plants have three elements, and then to prove that all three are one and the same. The pretended difference of function which confirms this division is of no importance, as there is not so much difference of function between vessels and cells as there is between two cells, the one of which secretes a volatile oil and the other granules of starch.

The milk-vessels (laticiferous tissue) which are covered with a proper membrane have not, with certainty, been made out to originate in cells. Their origin is obscure, and in their perfect state they resemble elongated branched cells, and agree with these in the transition forms which they exhibit in the progress of development.

§ 16. Up to a certain time the cell-wall grows in its entire extent, through intus-susception, but not often uniformly. Individual spots are more freely nourished, and form warty projections upon the external or internal surface of the cell.

It appears to me that the attention which this point deserves has not been given to it. It has been long known that certain hairs possess warts, which are clearly arranged in spiral lines. In most cases these warts are small and uniform in size, as on the hairs of the families *Boragineæ*, *Urticeæ*, *Malvaceæ*, &c. Sometimes, however, longer striped elevations of the external surface are seen, as in the anther-hairs of *Lobelia cardinalis*, the two-armed hairs upon the young branches of *Cornus mascula*, &c. But the most striking thing about these warts is, that they display one or two cavities in their interior, and are separated by a definite line from the surface of the hair, as though they were adherent cells. They are seen in the hairs of the throat of the species of *Anchusa* (fig. 15.) and other plants. These warty excrescences are not confined

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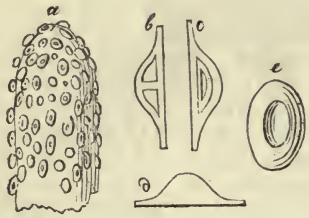


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to the external surface of hairs, but often form projections in the interior of hairs, as, for instance, in the so-called root-hairs of *Marchantiaceæ*, in the fibrous cells of *Peltigera canina*, in the spindle-shaped cells in the style of *Cereus phyllanthoides* (fig. 16.), in the medullary rays of *Pinus sylvestris*, in the hairs of *Malpighiaceæ*, where they form small peduncu-

[15] *a*, A hair from the nectary of *Anchusa italica*, covered with warts. *b*, *c*, *d*, Longitudinal section of warts (*e*), as seen from above.

[16] Hair, with warts upon it, from *Cereus phyllanthoides*. The cell-walls are irregularly thickened.

lated knobs*, and in the stinging hairs of the leaves of *Anchusa crassifolia*, where they appear as granular warts. Of the history of the development of these little knobs, especially those of the *Malpighiaceæ*, we know nothing.

§ 17. In some rare cases, as in the spores of some *Confervæ*, there are formed, sometimes upon the external surface of the cell and sometimes only at a particular spot, fibrilliform processes, which exhibit a vibratile motion similar to the cilia found on the mucous membranes of animals.

For the observation of this highly interesting phenomenon, we are indebted to the labours of Unger† and Thuret.‡ I have not yet had an opportunity of confirming these observations. The following is the result of their researches: — Thuret distinguishes four forms. In the *Conferva rivularis* and *C. glomerata* the spores have at their tapering ends two vibratile cilia. In *Chætophora elegans* var. *pisiformis* and another species there are four cilia. *Prolifera rivularis* and *P. Candollii* of Leon Leclerc (*Œdogonium* of Kützing?) have in the same spot a crown of vibratile cilia. In the last place, the *Vaucheria Ungeri* Thuret (*V. clavata* and *ovata* DeC.) have the entire surface of their spores covered with vibratile cilia. This last fact was first ascertained by Unger. Upon the origin of these cilia nothing is known, and just as little of the mode of their disappearance. Just as suddenly as these cilia disappear when the moving spore has fixed itself, do they appear when the spore leaves its spore-case. The perfectly formed spore-cells are brown in all cases, according to Kützing, but those which have the power of moving are green. According to the history of the development of the cells of *Algæ*, given by Nägeli, they originally consist of a closed sac of mucus, and subsequently there appears around them a membrane of cellulose. It might be a matter of inquiry whether the imperfect mucus-cells have not the power of forming cilia, which they lose immediately the proper cell-membrane is formed. The membrane bearing the moveable cilia would be then the same layer of mucus as, in the antheridia of the Mosses, *Hepaticæ*, &c., is transformed into spiral fibres, and which, in the cells of the *Characeæ*, *Naiadeæ*, and many higher plants, form little moving streams. Nägeli has also promised shortly an account of the relation between these movements and the nitrogenous contents of the bodies in which they occur.

§ 18. When the cell has reached a certain degree of development, an essential change takes place in its mode of nourishment: the newly formed cellulose is not taken up by intus-susception, but is deposited upon its inner surface as a concrete layer. This deposition does not, however, take place as a continuous membrane, but is formed in the direction of a spiral, as a spiral fibre or band. Should the cell distend after this deposition, then the spires which laid close together at first are drawn asunder. The less the cell is extended, the firmer is the union of these fibres with its walls.

* Morren, Obs. sur l'Epaississement de la Membrane végétale dans plusieurs Organes de l'Appareil pileux. (Bullet. de l'Acad. Roy. de Bruxelles, tom. vi. No. 9.)

† Unger, Die Pflanze in Moment der Thierwerdung. Vienna, 1843.

‡ Thuret, Recherches sur les Organes locomoteurs des Spores des Algées. (Ann des Sc. Nat., Mai, 1843.)

The individual spires of fibres, or particular spots of the spires, often grow together. From these circumstances a very varied configuration of the cell-wall results, which may be comprehended under two divisions. First, where the fibres are clearly separable (fibrous cells, *cellulæ fibrosæ*); and, second, where the fibres are so grown together, that they appear like a continuous membrane beset with little pores (porous cells, *cellulæ porosæ*).

*Nature and Origin of the Spiral.*—A spiral may be formed either from left to right or from right to left. If we take the distance from the commencement of the one spiral to the commencement of another directly above it, and make it *a*, then + *a* will be the expression of the spiral winding to the right, and — *a* that of the spiral to the left, and *a* — *a* the expression of the ring passing between them. The right spiral is the most frequent, but the left occurs often enough to render the resulting ring as indifferently the produce of either. It is, however, possible for the ring to have another origin. Each spiral may be divided into two halves, which, regarded from the same point, proceed in different directions. If the one half of the winding be from right to left, the other must be from left to right. Two spirals proceeding in the same direction would run parallel, but would cross each other on a flat surface (fig. 17. *c*). Two spirals running in opposite directions would cross each other twice in the course of one entire turn (fig. 17. *d*). This last form has not yet been observed. Link* thinks he has seen it, but his own drawing shows that it belongs to the first case. The lines crossing each other in the walls of the liber cells of *Apocynaceæ*, may be explained upon the supposition of there being two layers, lying one upon another, turning in opposite directions.

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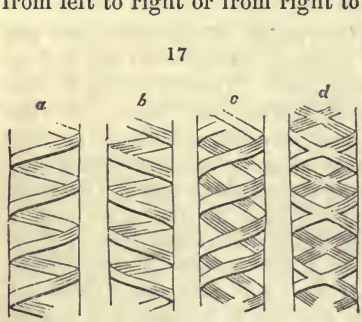


It is easy to perceive in the larger spiral fibres, when they are cut transversely, that they are homogeneous. In the old fibres of *Arundo Donax* they consist of a fibre lying on the wall, and one on each of the three free sides. In a transverse section, under a good microscope, it may be easily seen that the fibres are never round, but that they consist of a flat, thicker or thinner, band, whose free edge or side is, perhaps, at the utmost a little rounded. (Plate I. figs. 18, 19, 20.) The idea that they are hollow canals arises out of defective observations.

I do not believe that the first origin of the spiral has been observed. It appears to me that it exists much earlier than can be at present detected by our optical instruments, as it is formed from a matter which cannot be distinguished from the contents on the walls of the cell. The spires are more transparent in their earliest stages, and when invisible as a whole they may be observed as small projections upon the edges of the cell: in this state they are contracted, and are thus more bulky.

* Elementa Philosophiæ Botanicæ, p. 167.

[17] Diagram. *a*, Left spiral. *b*, Right spiral. *c*, Two left spirals in one cell. *d*, Two spirals right, and two left, in one cell.

Where they are perfectly invisible, the application of a little iodine will frequently make traces of them evident: spiral formations are also frequently observed, for the first time, when the vessels begin to carry air, on account of the different relation of the air and the solid substance of the vessel to light.

In addition, I find that in all spiral formations the spires are narrower the younger they are, and also more simple and unbranched in their structure: in the most abnormal forms—for instance, the annular vessels—I have found most evidence of this.* From these facts, then, it is to be inferred, that the foundation of all the forms of spiral formation are simple, unbranched, narrow, spiral fibres lying one upon another; and upon this simple hypothesis, combined with the undoubted fact that all spiral formations become first known to us after they have been present for a long time, and during this period have become considerably changed, we may easily explain all the phenomena observed.

It must, however, be confessed, that we are still far from being able to supply a rational induction for the phenomena of spiral formation: we have, even now, scarcely any indication of the relation which exists between the formation of a spiral and the nature of the plant or of the cell in which it occurs. We should gain a secure point for the development of the whole doctrine if we could find a single case, even a case which was not connected with the formation of a spiral fibre, in which we could prove, from the existence of a vegetable cell under certain circumstances, that a tendency to a spiral direction must necessarily follow. Could we trace the spiral direction of the circulation in the central cell of *Chara* to a peculiarity in the nature of the cell as a necessary consequence, then we should obtain for all spiral phenomena an entirely different signification. In looking at the peculiar brown-coloured spiral fibres in the cells of the sporidia of the *Jungermanniæ*, the movable spiral fibres in the antheridia of Charas, Mosses, *Jungermanniæ*, and Ferns, it appears to be not improbable that we include under the name Spiral Fibres very different things. In these instances, the one is a peculiar form of the deposit layer of cell-membrane, a non-azotised substance (cellulose); and in the other, an especial form of the mucus, the nitrogenous constituent of the cell.

*Forms of the Spiral.*—After the spire has been developed in a cell, the latter often becomes extended.

*A.* This extension produces the following modifications:—

*a.* When the turns of a single fibre early grow together so as to form a ring, whilst the free fibres become torn or resorbed, so that the cell exhibits either the rings alone, or mixed with single turnings of the spire, these rings are ordinarily little or scarcely at all connected with the cell-wall (*Cellulæ annuliferæ*) (fig. 18.).

18

This occurrence has been observed in its entire course in the stem of many *Tradescantiæ*, in the root-stock of *Equisetum arvense*, and in some other plants. In many other plants I have failed in detecting the first formation of the rings. In the *Cactaceæ*, in which the rings are so large, I have not been able to observe their formation.

* Notwithstanding Mohl's objections (Flora, v. 1839, Nos. 43, 44.), I still, after repeating my observations, hold the view I took at first. (Ibid. Nos. 21, 22.)

[18] A fibrous cell, with two single rings, from the neighbourhood of the woody bundles of the *Opuntia peruviana*.

*b.* When simple or compound spirals do not grow together and form rings, but the cell continues to grow, the spirals are then found in the cell more or less free (*Cellulæ spiriferæ*) (fig. 19.).

*c.* When many fibres grow together longitudinally, or the individual turns unite at different points, and the cell grows rapidly, the free parts

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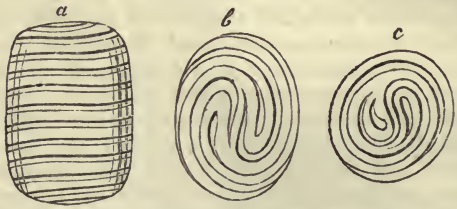


of the fibres are drawn away from each other. The more numerous the points of adhesion, the less the cell extends itself, the firmer grow the fibres to the cell-wall * (*Cellulæ retiferæ*) (fig. 20—23.).

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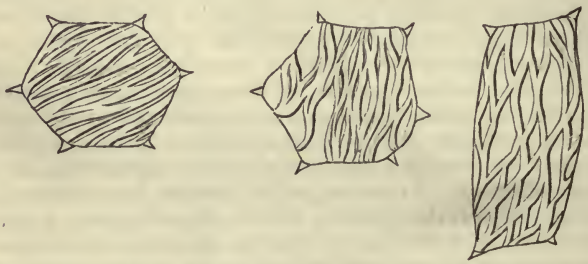

*B.* When the cells, from the first moment at which the spiral fibres are produced, cease to extend, the turns of the spire grow firmly together to the original walls of the cell. In this case the fibres touch each other at countless points, and grow together. It is seldom that the spires unite throughout their whole length to form a homogeneous layer; yet this occurs sometimes, as seen in the cells of the liber of the Flax and the Lime (*Tilia europea*). This sometimes takes place on one side of a cell, whilst the other exhibits a formation of pores, as in the rows of great porous cells in the vascular bundles of Monocotyledons. In most cases, however, the spires grow together at particular points, leaving between them smaller or larger openings in the disunited spaces (fig. 23.). Frequently the corners of these openings become rounded by the deposition of fresh matter, and the original chink appears as a little pit in the deposit-layer (fig. 24.). In tolerably thick deposit-layers this pit, by a transverse section, may be observed as a narrower or wider canal (fig. 24.), which sometimes gradually or suddenly opens at the outside of the wall of the

* To this form belongs the branched spiral of authors.

[19] A fibrous cell, with 1—3 pure spiral bands; *a* seen from the side, *b* and *c* from above. These cells are found under the epidermis of the leaves of *Pleurothallis ruscifolia.*

[20] Fibrous cells, with netted fibres, formed from a spiral, as seen in the veins of the leaves of *Gesneria latifolia.*

[21] Netted fibrous cells, from the back of the root of *Maxillaria atropurpurea.*

[22] The same from the root of *Acropera Loddigesii.*

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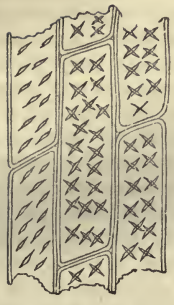

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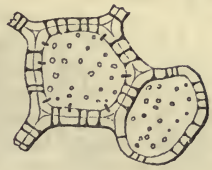

cell (fig. 25.). In the woody tissue of the *Coniferæ*, in the porous vessels of the wood, in almost all vessels with oblong pores, the pore may be seen surrounded by a double circle, an inner one easily recognised as the pit in the deposit-layer, and an outer wider circle (fig. 26.).

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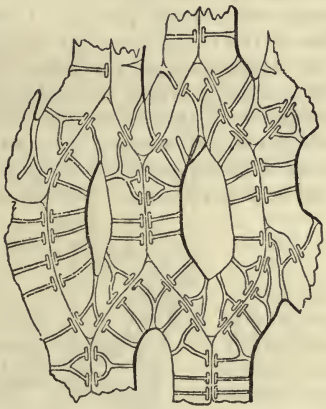

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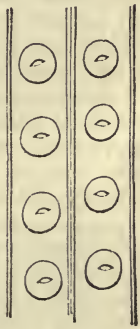

Sometimes three circles are seen. If we compare the transverse section of these pits with their appearance on a flat surface, we shall see how this takes place (fig. 27.). In the region of the canal of the pore, the cell-walls, which at first lay upon one another, become separated, and leave a lenticular space between them, which is filled with air. The edges of this space appear from the surface as an external circle. The one or two inner circles are produced by the canal, as seen in fig. 27. This appearance of the external circle admits of two explanations: 1st, its greater

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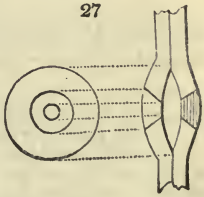

[23] Porous cells from the parenchyma of the stem of *Arundo Donax*.

[24] Porous cells, from the petiole of *Hoya carnosa*.

[25] Porous cells of the petiole of *Cycas revoluta*. Small pores are found where the cells are united to each other, but large ones where the cells open into the intercellular passages.

[26] Porous cells from the wood of *Abies excelsa*. The pores are surrounded by a large external circle.

[27] Semidiagrammatic. A single perfectly developed pore from the wood-cells of

distance from the pore, when seen together with it from the plane surface, is diminished (fig. 28. *a*, *b*); and, 2dly, the thickness of the air-clefts between the cell-walls; for if these are very flat, the bordering surfaces will appear almost parallel, and the edge is either not at all or in a very slight degree darkened, so that it cannot be observed. If these cases are placed in profile, as in fig. 28. *a*, *b*, *c*, *d*, this explanation will be understood. If we examine the process of development in the large and easily observed porous vessels of the cambium of the Willow, the Lime, the Poplar, and the Maple, we shall find that all of them present dark spots, which resemble those of the external circle of the air-clefts: a clean transverse section of these spots is difficult to obtain; but, from our knowledge of optical phenomena, this dark spot may with certainty be referred to the presence of a bubble of air. At this time no pore is present: this is generally formed at a subsequent period. If these facts are placed together, we may arrive at the conclusion that the air-cleft is universally present previous to the appearance of the pore. The consequence is, that, as the changes of matter by which the cell is nourished can only take place during the contact of two cells, the cells are not nourished at those points where the air exists between their walls: thus the pore and its canal originate as a partial atrophy of the cell-wall. Therefore, in all the transitions between porous cells through the netted

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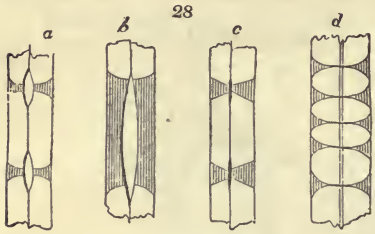


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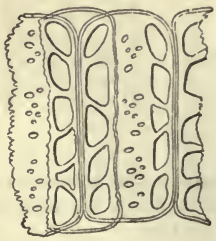

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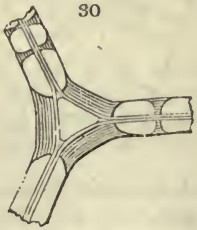

cells into the pure spiral, we must seek the cause of the division into separate spirals—not in the cell itself, but in its circumference. This

*Schubertia disticha*, seen from the surface and in transverse section. The dotted lines explain the relation which the two aspects bear to each other.

[28] Semidiagrammatic. Transverse sections of the pores. *a*, Pores small, in relation to the spot where the neighbouring cell-walls separate from each other. *b*, Pores large, in relation to this spot. *c*, The separation of the cell-walls so small that it only appears as a black streak. *d*, The separations not observable between the cells are apparently homogeneous layer rings, in which the pores terminate.

[29] Porous cells from the perispeum of the ivory nut.

[30] Transverse section of an intercellular passage, with the three portions of cell-wall which forms it. The larger pores in the deposit-layer of the intercellular passages, as well as the smaller ones on the double cell-walls, are seen. The corners of the intercellular passages are rounded off by a peculiar deposit.

is offered as an explanation of the facts, to guide farther inquiry, rather than as a true law of development. There are two cases which seem to form exceptions to this view. The first is the formation of pores, which open into intercellular passages independent of the neighbouring cells. These are very beautifully seen in the petioles of the *Cycas revoluta*. In this case the single wall is easily affected, and the intercellular passages, filled with air, act in the same way as the air-clefts. We frequently see, also, a great air-cleft, forming a large fissure-like pore on one side, and many little pores on the other side, as is frequently seen present in the porous vessels of the *Balsamineæ*. In a similar manner the porous cells of the medullary rays in various species of *Pinus* often exhibit a longitudinal air-cleft, which resembles the pores in many cells.

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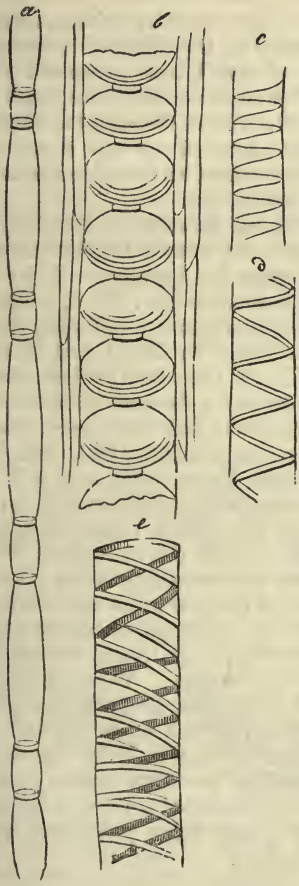


The last form worthy of mention is when the cell-walls do not extend, and the spires touch each other, but do not grow together. This is the form on which Meyen founded his false theory of the fibrilliform nature of all cell-membrane. This phenomenon often presents itself, as in the cells of the parenchyma of the tubers of the Dahlia (Plate I. fig. 26.), the hairs of the young leaves of *Cycas revoluta*, in the hairs of many *Mammillariæ* and *Melocacteæ*, the scales of the buds of *Pinus sylvestris*, &c. Sometimes the spires in these cases present fissures, as is beautifully seen in the cells of the rootlets of *Oncidium altissimum* (Plate I. fig. 24.).

*Individual Development of the Spiral Fibres, and of Abnormal Forms.*—Every spiral fibre at its first visible existence is a fine thread, which increases both in breadth and length (fig. 31. *c*, *d*.). This goes on so long as the cell contains sap, but ceases immediately this is absorbed, and the cells fill with air. In some cases a part of the spiral fibre does not increase with the rest, and the fibre terminates as it were with a pointed end, as is often seen in the vessels of the common gourd (fig. 31. *e*.). Occasionally, and apparently from disease, the cells which had originally been filled with fluid, and which had given place to air, are again filled with fluid when a fresh set of anastomosing spiral fibres are formed. This

[31] *a*, Annular ducts from the stem of *Canna occidentalis*, with a regular distance of the rings. *b*, Annular ducts from the petiole of *Musa sapientum*, the vessel between the two rings being distended. *c*, *d*, Spiral from a cactus, very young, and perfectly developed. *e*, A spiral vessel from *Cucurbita Pepo*, with some of the spiral fibres ending in a point.

takes place in the old stems of *Scitamineæ*, and of speces of *Commelineæ*, as in *Hedychium Gardnerianum*, and *Tradescantia crassula*. Another regular formation of anastomosing fibres occurs between the spires of neighbouring cells. This may be seen in the large knotted vessels of many *Balsamineæ*. In these may be seen a perfectly regular spiral fibre with a slight yellow colouring, but accompanied by another short, almost colourless, vertical branch, which is easily recognised by its transparency. If this is traced it will be found to follow accurately the course of the commissure between the two vessels, and to form a kind of bridge over the commissure from one fibre to another. This clearly does not belong to the original spiral formation. Its constant appearance in porous vessels, with long transverse clefts, has caused it to be called scalariform tissue.

In the last place the annular ducts present some striking phenomena, amongst which must be reckoned the constancy of the distance between the same annuli. A remarkable instance of this I have observed in *Canna occidentalis*, where a short distance between the annuli regularly alternates with one three times as long (fig. 31. *a*.). In the annular ducts of the petioles of *Musa paradisiaca*, I have observed the cell between the two rings to be remarkably distended and swollen, so that there could be no union with the rings of cells near to each other.

*Historical and Critical Remarks.*—The spiral fibres were early discovered by Malpighi and Grew, or perhaps even sooner by Henshaw. Bernhardi (Ueber Pflanzengefässe und eine neue Art desselben: Erfurt, 1805) and Moldenhauer (Beiträge zur Pflanzenanatomie: Kiel, 1822) pointed out the existence of the external cell-membrane enveloping the spiral fibre. The annuli or rings were discovered by Bahel, and their enveloping membrane by Bernhardi. (See Link, Elementa Philosophiæ Botanicæ, ed. sec. tom. i. p. 27. 169.) The porous cells were discovered by Leuwenhoek (Opera omnia, tab. 462. fig. 20.); but they were first correctly estimated by Mirbel (Histoire Nat. des Plantes, 1800, tom. i. p. 57.; Traité d'Anatomie et de Physiol. végét., Paris, 1802, t. i. p. 57. fig. 1—4.). He was at first opposed till Hugo Mohl published his observations confirming Mirbel's views (Ueber den Bau der Ranken und Schlingpflanzen, Tüb. 1828). Mohl also discovered the membrane investing the porous cells (Ueber die Poren des Pflanzenzellgewebes, Tüb. 1828). These are the most important steps in the history of our knowledge. What remains is the notice of the more or less frequent occurrence of one or another modification. Meyen (Physiologie, vol. i.) has collected a large mass of information on the whole of this subject. Valentin (Repertorium, vol. i.) was the first to contend that all these formations originate in the spiral. Link (Elementa) maintains that the pores and clefts are portions of torn spiral fibres. Mohl is of opinion that the annular ducts are primary formations. Hartig (Beiträge zur Entwickelungsgeschichte der Pflanzen, &c. Berlin, 1848) has announced a view of spiral cell development which cannot be regarded as any thing more than an ingenious fiction, it having no foundation in facts.

§ 19. Generally, the deposit-process forms a new layer on the wall of the cell of the same form; but cases occur in which on the one side of the wall it unites a spiral fibre to a homogeneous membrane, whilst on the other it excavates a spot for a fissured pore

(here belong the so-called porous vessels of the wood); or in one part of the cell it becomes changed to rings, whilst in another part it becomes spiral, netted, or, what more frequently happens, it remains entirely porous.

To this point too little attention has been given. We know in this relation only the last modification, the mixed tubes (*tubes mixtes*) of Mirbel. Here, however, belong also the so-called porous vessels of our dicotyledonous woods, which, in the manner in which they are spoken of in books as tubes formed of an entirely porous membrane, certainly do not exist. All these so-called vessels are only so far porous as they touch one another; as, where they project on the wood-cells, these walls are often almost entirely homogeneous, and exhibit scarcely a trace of pores. This may be easily seen if the individual cells are isolated by means of nitric acid. When these vessels are arranged in radial rows, but never or very seldom when they lie laterally on one another, if we cut them directly across we shall find very evident porous walls, but never or extremely seldom are they to be seen by a longitudinal section. This is the case in the *Coniferæ*, where the pores predominate (but not exclusively) on the side next the medullary rays; or in the *Hibbertia volubilis*, where they appear, on the contrary, towards the pith and the bark, seldom towards the side of the medullary rays; so that the two other sides in these cases have a homogeneous development.

§ 20. The process of depositing layers is often repeated during the life of a cell. *a.* Each successive layer is generally deposited accurately upon the preceding, ring upon ring, spiral upon spiral, porous layer upon porous layer. *b.* But in some less frequent cases the deposit takes place according to the circumstance of the cell; so that when, through extension, the cell-fibres become separated, the extension causes the deposit of a porous layer. Ordinarily, also, the direction of the spiral in the following layer is the same as in the foregoing, but in some cases the direction of the next spiral is directly opposite that of the first.

The first condition mentioned above is very common, and rings are often found so very much thickened that they have only a little hole in the centre; and as they do not increase so much in breadth, they appear, when perfectly formed, like thin discs with a hole bored through them. They are seen in the *Cacteæ*, as *Opuntia cylindrica*, *Melocactus*, *Mammillaria*, &c. This occurrence is also very frequent in porous cells, so that the cavity of the cell is reduced to a scarcely visible point. Such cells are very common in plants, and a single layer may be easily seen upon a transverse section. The pores of the deposit layers become gradually converted into canals (fig. 32.). Such canals frequently approach each other, and at last unite, so that the inner layer is much less porous than the outer (fig. 33.). With these may be compared the elegant formations in the so-called

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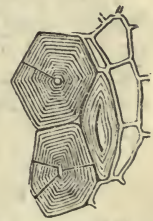

[32] Transverse section of three liber-cells and some parenchyma-cells in the *China regia* (*Cinchona scrobiculata* Humb.). The liber-cells show very clearly the deposit layers and the porous canals.

stones of winter pears and quinces; in the bark of the petiole and stem of *Hoya carnosa*; in the stem of *Fraxinus excelsior* (Plate I., fig. 22.); and in the fruit stalks of *Magnolia* (Plate I., fig. 21.), &c. These are called, with peculiar impropriety, branched porous canals. Mohl* was the first who discovered this process of growth by deposit-layers in the cells of the plants, and thus explained one of the most important processes in the life of the plant.

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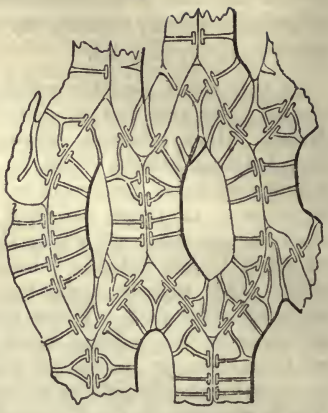

Formations of the second kind have been longer known, as in the wood of the Yew, where separated spiral fibres and rings are seen, between the windings of which are also large pores. In recent times many similar formations have been observed in the Lime, the Vine, in *Prunus Padus*, *Helleborus fœtidus*, &c. (fig. 34.). Little is at present known of their mode of formation. In the Lime, in the spring, we find in the cambium spiral cells with the fibres close together; in the course of growth these extend, the spires separate from one another, and pores are formed between them, so that here the porous layer is the last formed. How it is formed in other cases is yet a question.

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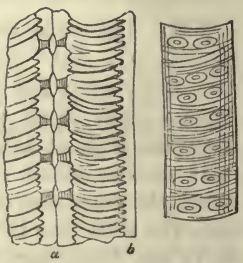


In the tender spiral cells of the bark of the *Asclepiadeæ* and *Apocynaceæ*, and in the delicate spiral cellular tissue generally, there is sometimes observed the appearance of a crossing of the spiral fibres. This may arise from the spires of neighbouring cells, or from the transparency of the walls of the same cell; but there can be no doubt that in some cases it is an original formation (Plate I., fig. 23.), and arises probably from spires formed in opposite directions.

§ 21. In many cells the spots remaining free from the secondary deposits become fluid and are resorbed. In this way cavities are formed in the membrane. Upon this depends the distinction between cells and vessels. The last are only rows of cells whose cavities have in this way been brought into union with each other.

* In his work on the structure of the palm-stem, and in other places.

[33] Porous cells of the petiole of *Cycas revoluta*. Small pores are found where the cells are united to each other, but large ones where the cells open into the intercellular passages.

[34] Vessels from *Helleborus fœtidus*. *A*, Longitudinal section. *a*, Two adhering vessels with the pores cut through, and the projections of the spiral fibres. *b*, The wall of the vessel, without pores touching the wood-cells, with the projections of the fibres. *B*, A vessel seen from without.

Hugo Mohl was the first to point out the distinction between these excavations and pores; and daily observation confirms the existence of actual cavities in the membrane. The existence of a free communication between the vascular cells was early recognised; but they were regarded as originally continuous tubes, and wonderful views of their structure announced, because the history of their development was not studied. All vessels consist originally of vertical rows of closed cells, in which are gradually deposited the secondary layers, according to the forms of which they are named. When these deposit-layers are tolerably perfectly formed, a process commences whereby the primary cell-membrane is resorbed, so that the individual cells are brought into free communication. This resorption generally includes all horizontal formations of the deposit process, but in some cases a horizontal wall remains with only a pore or hole in its centre (fig. 35.). Such formations present themselves very decidedly in the Mosses in the group *Leucophaneæ*, as in *Sphagnum*, in the parenchyma-cells of old *Cycadeæ*, in the so-called vessels and sometimes porous cells of *Coniferæ*, where they touch the medullary rays, in the green-walled cells of the root-caps of *Aerides odoratum*, &c.

35

## SECTION II.

### OF CELLS IN COMBINATION, AND INTERCELLULAR FORMATIONS.

§ 22. The individual cells, originating in the manner described, are grouped together in various ways into great masses (called tissues, *tela, contextus*), which, according to their combination out of various or similar elementary parts, may be arranged on the following plan: —

§ 23. *A.* PARENCHYMA. — It forms the principal mass of plants and of their parts. It is,

*a. Incomplete Parenchyma,* when the cells barely touch each other by their parietes. This may be again divided into,

1. *Spherical or elliptical Parenchyma,* in which the cells are round. This prevails in succulent plants (fig. 36.).

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[35] Porous vessel from *Arundo Donax*, in which a portion of the outer wall is removed, exposing the point of union of two cells, where a horizontal wall, with a large hole in it, is seen.

[36] Imperfect elliptical parenchyma from the leaf of *Acrostichum alcicorne*. The adhering surfaces are porous.

2. *Spongiform Parenchyma,* which consists of cells extending themselves irregularly in a stellate form, and which touch only at the end of each ray (fig. 37.). Such tissue frequently fills up the air-passages, and occurs in all tissue which dries rapidly, and also in the under half of the parenchyma of most leaves.

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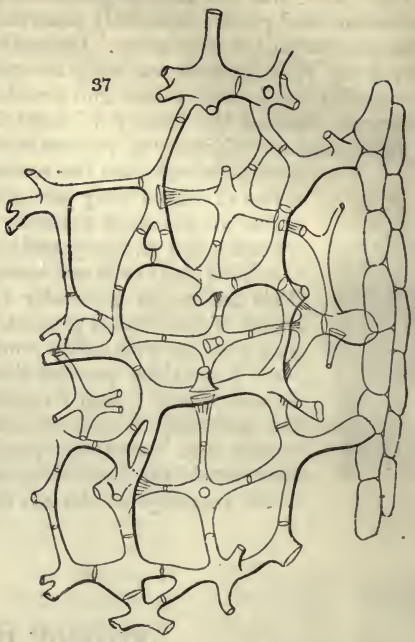

*b. Complete Parenchyma,* in which the touching of the cells is complete on every side.

1. *Regular* or *dodecaedral parenchyma,* consisting of almost pure polyedral cells, without the predominance of any particular dimension. It is found mostly in the pith of plants (figs. 38, 39.).

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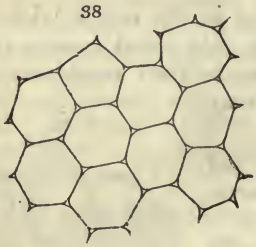

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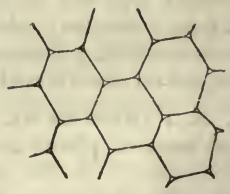

2. *Longitudinal, cylindrical,* or *prismatic parenchyma.* It occurs in rapidly growing plants, sometimes in the pith of monocotyledons and in the interior of species of *Fucaceæ* (fig. 40.).

3. *Tabular parenchyma,* consisting of four-cornered tabular cells. They occur in the external bark, especially in the suberous and cellular layers (fig. 41.).

[37] Spongiform parenchyma from an incomplete intercellular passage of *Canna occidentalis.*

[38] Transverse section of the parenchyma of the stem of *Balsamina hortensis.*

[39] Longitudinal section of the same.

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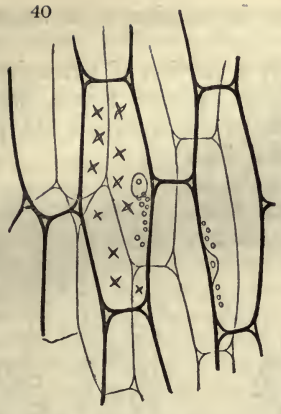

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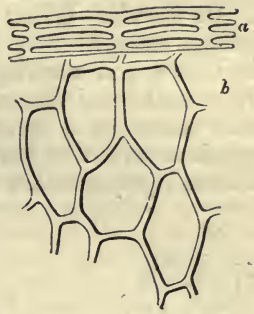


§ 24. *B.* Intercellular System.—The contact of the sides of the cells in plants is seldom or never perfect, so that there are formed numerous cavities, of which the following are the most important varieties:

*a.* Original cavities formed by the imperfect contact of the cells:

1. *Intercellular passages;* small three-cornered canals running around the cells, and seen in almost all kinds of parenchyma.

2. *Intercellular spaces;* great irregular spaces between the cells, occurring especially in spongiform cellular tissue.

*b.* Later-formed cavities:

1. *Receptacles of special secretions.* These arise from the exudation of the juices of the cells into the intercellular passages. Two kinds of these may be distinguished:

*α.* Formed by compact cells, lying close on one another, and apparently not separable; as the resin-cells of the bark of *Coniferæ*, and individual gum-cells.

*β.* Formed by loose cells, with their walls projecting vesicularly into the cavity, and apparently separable. Such cavities mostly contain peculiar secretions, and are seen in the latex-canals of species of *Mammillaria* and *Rhus*, the gum-cells of *Cycadeæ* (fig. 42.), and the resin-cells of the wood of *Coniferæ*.

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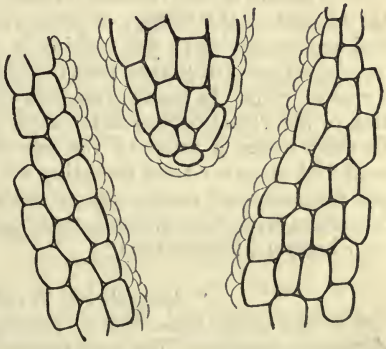

[40] Parenchyma from the stem of *Vicia Faba.* In the cells are seen porous openings, and in two cells cytoblasts, with granules of starch.

[41] Parenchyma from the bark of *Quercus Suber* (cork oak). *a*, longitudinal section. *b*, as seen from surface.

[42] Tissue from the opening of two dextrin passages in the petiole of *Cycas revoluta.* The compact parenchyma is clothed with a delicate vesicular tissue, projecting into the cavity.

2. *Receptacles of air*, formed by the destruction of a mass of parenchyma. They are:

*α*. Air Canals. These are formed by a portion of parenchyma becoming changed first into spongiform cellular tissue, which is then torn and resorbed. The walls of these canals are perfectly smooth, and the cavity is divided into definite spaces by a layer of stellate cells, as though interrupted by horizontal layers. Seen in *Canna, Nymphæa*, &c. (figs. 43, 44, 45.).

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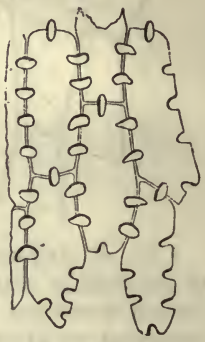

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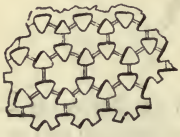

*β*. Air Cavities. In these a portion of parenchyma is inordinately torn by the growth of a portion of the plant. Their walls are rough with the remains of torn cells. Seen in the stems of grasses, many *Compositæ*, and in the *Umbelliferæ*.

§ 25. *C.* Vessels. (*Vasa, Tracheæ.*) When a row of lengthened parenchyma-cells have, through resorption, their cavities brought into continuous communication, such a series of cells are called, by an unfortunate expression, a vessel; and it is distinguished from the above tissues by different names, according to the nature of its walls, as spiral vessel, annular duct, porous vessel, &c. (*vasa spiralia, annulata, porosa*).

The nature of the vegetable vessel has been much misunderstood, from the neglect of the history of its development. Various views have been and are entertained; yet nothing is easier, in the larger and more fully developed parts of plants, than to observe the formation of a vessel out of a row of cells. In many cases, however, it may be difficult, as the formation of the vessel occurs at too early a period in their history to be seen. In other cases, a union of the two vessels, side to side, may prevent an unskilful observer from detecting what is going on in them. Nowhere is the formation of vessels out of cells, and the connexion of the spiral formation with this process, more easy to be observed than in the common balsam (*Balsamina*).*

* Anatomie und Physiologie der Cacteen.

43 Stellate cellular tissue, from the horizontal layers in the air-canals of the petiole of *Aponogeton distachyon*. The three-cornered intercellular passages are very large, and the rays of the cells proportionately long.

44 The same. The three-cornered intercellular passages are somewhat rounded, and rather small; the rays of the cell proportionately short. The walls of the cells, between two rays, are somewhat thickened.

45 The same from the leaves of *Pilularia globulifera*. The cells are somewhat lengthened, with short and broad rays; the parts of the wall in contact thickened; the intercellular passages irregularly rounded.

Frequently, in the later-formed vascular cells, the septum is broken down in such a manner that it remains in a circle as a small edge. This septum is seldom entirely horizontal, but ordinarily somewhat inclined from the axis of the plant towards the radius, very seldom towards the periphery. Such cavities in the septum may be frequently seen by a longitudinal section of a vessel. Treviranus* first remarked this, but knew not what to make of it. Meyen † gave a very unsatisfactory explanation of it. This breaking up of the septum only occurs where there is a kind of resistance on the part of the septum itself. Where this tendency is very strong, instead of a single cavity many are formed, and the septum acquires a regular ladder-like aspect; a fact first announced by Mohl. ‡ Examples may be seen in the Beech, in the roots of Palms, in *Arundo Donax*, &c. Again, the tendency may be so strong, that the cells may be regarded as lying on one another, and there is formed upon the septum, according to the nature of the cell, spiral fibres or pores.

That the completely developed vessels contain only air, is a fact that can be ascertained by the naked eye. Sometimes, in old age, abnormal fluids will be found in them, and cells are developed in the vessels. Cells are found in the old porous vessels of the Oak and Elm, and I have found them frequently in the spiral vessels of the stems of *Scitamineæ*, as *Canna* and *Hedychium*. Such cells do not appear to me to originate in the vessels, but arise from neighbouring cells being pressed into the vessel between the spiral fibres. The cell thus pressed into the vessel originates the new cells. The so-called moniliform vessels are not formed in a different manner from others.

§ 26. *D.* Vascular Bundles.—This term is applied to a mass of lengthened cells, of which a part have been changed into vessels, and which is more or less clearly distinguished from the *parenchyma*, which they penetrate in longer or shorter masses. They are either,—

*a. Simultaneous vascular bundles*, when all parts of the bundle originate and are developed at the same time, as seen in the *Cryptogamia*.

*b. Successive vascular bundles*, when the individual parts of the bundle, and especially in the stem, arise and are developed from within outwards. At first they consist of a delicate cellular tissue, filled with an opaque fluid (*cambium*), which, whilst internally it forms lengthened cells and vessels, goes on increasing externally. These may be divided into,—

1. *Definite or closed bundles.* In these the growth of the bundles only continues for a short time; they then become surrounded by a sharply defined cellular tissue, and are incapable of further development. Ordinarily the vessels lie in a line, or are formed from within outwards; externally, or on both sides the line, are seen a pair of large porous vessels, and the whole is surrounded and mixed with lengthened thick-walled parenchyma, which distinguish the

* Vom inwendigen Bau der Gewächse, Göttingen, 1806, tab. i. fig. 10. b.
† Phytotomie, S. 264.
‡ De Palmarum Structura, tab. N. figs. 13, 14, 15.

bundles from the thin-walled short parenchyma around. Such are monocotyledonous vascular bundles.

2. *Indefinite or unclosed bundles.* In these the cambium does not cease to develop, and the vessels to thicken from within outwards, till the organ, or the plant to which it belongs, ceases to live. Such are dicotyledonous vascular bundles, and they may again be distinguished into,—

*α.* Primary vascular Bundles, those which are produced during the first period of vegetation, or first year. In the inner half it consists of the same parts as the closed bundles, only that the vessels are more numerous, and not so regularly arranged; the outer half is composed of cambium-cells, which are distinct laterally and in front, but pass quickly into the surrounding parenchyma.

*β.* The Wood. After the completion of the first period of vegetation, the parts of a plant generally cease to increase in length; but as the new cambium-cells must, nevertheless, extend to a certain length, they necessarily interpenetrate amongst each other by pointed extremities. Thus originates, in the place of parenchyma, a peculiar tissue which is called *prosenchyma.* A part of these retain their narrow lengthened form, pointed above and below (wood-cells, woody fibres), but between them open individual perpendicular rows of cells, often very strongly marked, which become converted into vessels. The only exceptions to this are the *Coniferæ*, *Cycadaceæ*, and some others, where all the wood-cells are tolerably uniform. The portion of wood that is formed first in every year is composed of broad thin-walled cells, and contains more vessels than later-formed wood, which consists of smaller vessels, and the cells are always narrow and thick-walled. In this way the difference between the growth of the earlier and later periods of the year may be detected by the naked eye. It is from this cause that the trunk of a tree displays, on a transverse section, as many concentric rings as the tree is years old; and these are called *annual rings.*

The cellular tissue existing between the vascular bundles and their developing masses, and which ordinarily appear extended from within outwards, are called *medullary rays.* Such extensions of the cellular tissue are *large* when they reach from the pith to the bark, and *small* when they begin or end in the wood.

*The Cambium.* — When the growing parts of plants which form and develope buds are examined, there will be found always present a tissue which is only difficult of recognition in its individuality. The cells of this tissue, distended with assimilated mucilaginous granular matter, contain young cells, cytoblasts, and often also superfluous nutritionary matter, such as starch; and are pressed by small narrow delicate cells, so that it is very difficult in this tissue to distinguish its component parts. Gradually, separate masses of cells, with a distinct and definite outline, appear in this chaos, and they cease to partake of the process of growth going on. At first the epidermis is separated, then the vascular

bundles, later the parenchyma, and at last there remains a portion of cambium at the point of the stem (*Punctum vegetationis*, C. Fr. Wolff), and externally to the vascular bundles. This last part has been more especially characterised as cambium, but it does not differ from the other. The cambium is not an unorganised mass, as was formerly supposed, but in the vascular plants, at least, is always a cellular tissue containing cytoblasts, and, in a state of active vitality, forming new cells, a part of which adheres in all its forms to the cellular tissue already formed, and a part remains as cambium to carry on the process of growth. In this cambium the following tissues originate: —

*The Vascular Bundles.* — A large series of observations prove that the vessels, and to a certain extent the cells connected with them, cease to exhibit the collective energy of cell-life sooner than the neighbouring cells. They cease earlier to develope new cells, they pass sooner from the condition of the general nutrition of the membrane into that of the deposition of secondary layers, they consume quicker their assimilated contents without forming new ones, and when the neighbouring cells are first commencing their chemical activity they have either consumed all their juices, or convey only air (the vessels) or a very homogeneous indifferent sap (the young wood-cells). There are cells which pass through all the stages of life quicker than the parenchyma-cells. In this way all the phenomena may be easily and perfectly explained. The parenchyma-cells form new cells when the vascular bundles have ceased to do so. There will, therefore, be always present, in a longitudinal mass, a larger number of parenchyma-cells than cells of the vascular bundles; the last are always much longer than the first. This antagonism is especially evident at the commencement of a vascular bundle, at least at its sides, where its cells gradually pass into the parenchyma. As the formation of the secondary layers is an important point in the permanent development of cells, so the form of individual cells of the vascular bundles depends on the period in which they originate. Several kinds of vascular bundles are recognised.

1. In the higher *Cryptogamia*, the Ferns, *Lycopodiaceæ*, *Equisetaceæ* (cryptogamic vascular plants), sometimes in aerial stems (less in the creeping subterranean stems, and in the *Equiseta* generally), the entire vascular bundle arises and is developed at the same time. In these vascular bundles there is a great similarity of form; and, as the stems of these plants increase little in length after the formation of the vascular bundles, almost the only kind of vessel seen is that with cleft-like pores.* The *Lycopodiaceæ* have vessels with a very narrow spiral fibre; the *Equisetaceæ* † annular vessels, but with narrow rings.‡

2. In the *Phanerogamia* a successive formation of vascular bundles takes place. The parts next the axis are first developed from the cambium, and the development extends gradually towards the periphery. Then appear the parts belonging to the vascular bundles, but never until the other portions have made considerable progress. From this arises several important modifications of the vascular bundles. The type of the deposit layer depends on the nature of the vessel at first. Nearest the axis we find distant annular vessels; following these, vessels

* Mohl de Structura Caudicis Filicum arborescentium. Munich, 1833.

† They ought to be placed highest among the *Cryptogamia*, according to my view.

‡ Bischoff, Die kryptogamischen Gewächse. Nürnb. 1828.

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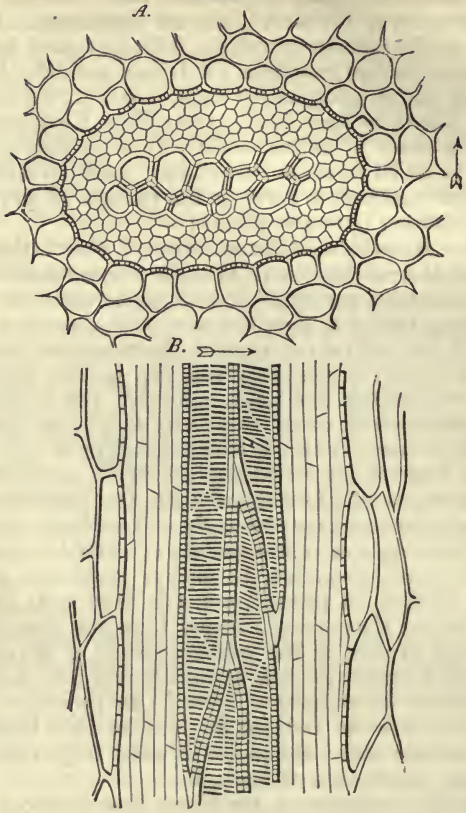


with rings less distant; then spiral vessels succeed, whose spires, although far apart, are yet not so far apart as the rings of the annular vessels; then follow closely-wound spiral vessels; then reticulated; and lastly, porous vessels. This course is observed although one or more of these formations may be absent. So constant is this structure, that the relative age of two vessels may be easily indicated by it. Thus in monocotyledonous plants we often see porous vessels lying at the side, or behind, the spiral and reticulated vessels, but they arise later than the others, and this is shown by their configuration.

*a.* In Monocotyledons, a remarkable change takes place in the cambium within a year of the first period of vegetation. At the commencement the cells which contained cytoblasts lose them, and their place is taken by a clear fluid, and all new formations cease, and the cells become arranged in perpendicular rows, so that where from three to five cells

[46] Simultaneous vascular bundles from the stem of *Polypodium ramosum.* *A*, Transverse section. *B*, Longitudinal section, through the smaller diameter of the vascular bundle. The arrows show the direction from the centre to the periphery of the stem. The thickened, somewhat lengthened, parenchyma which lies upon the vessels, surrounds a thickened, very lengthened, parenchyma which represents the cambium in monocotyledons.

were heaped together, a row of stronger, thicker, and longer cells are found (fig. 47.).*

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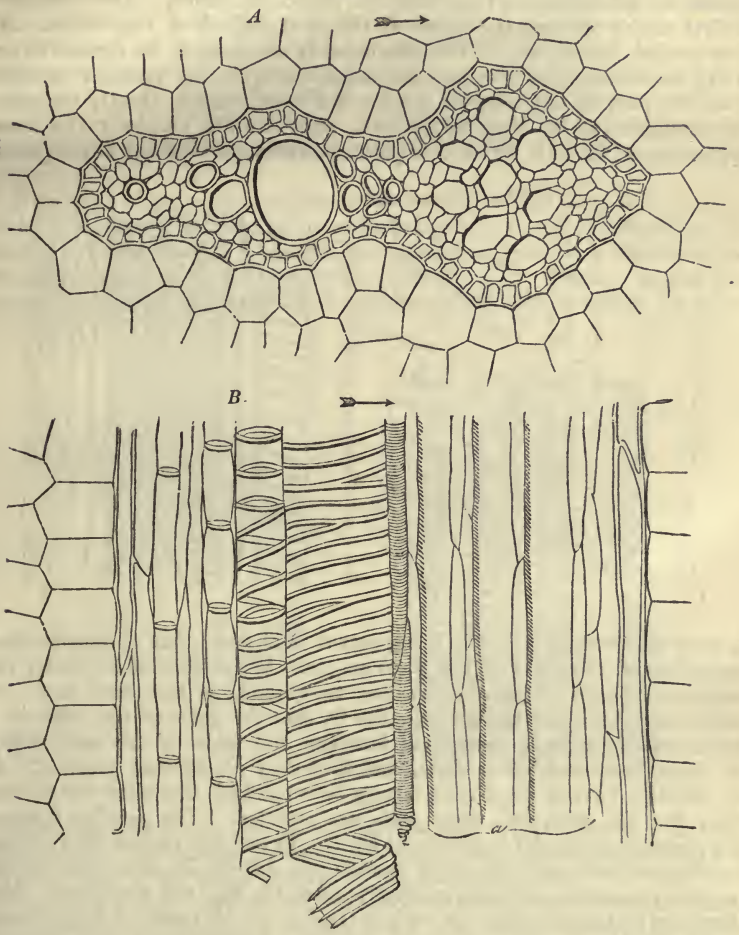


During this time the longitudinal parenchyma-cells belonging to the vascular bundles, and which either surround them, or form a great bundle both before and behind, have their walls strongly thickened, so that the unchanged vascular bundles are rendered much more apparent in the

* See Mohl de Palmarum Structura, where there are many drawings of monocotyledonous vascular bundles, but which do not express strongly enough the above peculiarity.

[47] Successive closed vascular bundles from the petiole of *Musa sapientum*, from a horizontal wall between two air-passages near to the under surfaces of the petiole. *A*, A transverse section. *B*, A longitudinal section of the same. The arrow denotes the direction from the upper to the under surface of the petiole. *a*, The cambium cells (*Vasa propria* of Mohl).

surrounding parenchyma (fig. 47.). Still, examples are very frequent in which the vascular bundles pass into the surrounding parenchyma.

*β*. In the earliest stages the vascular bundles of the Dicotyledons cannot be distinguished from those of Monocotyledons. The difference is first visible towards the close of the first period of vegetation. At this period the aspect of the cambium is unchanged, its formative activity continues, and new cells are deposited upon the vascular bundles. The first part of the vascular bundle is formed under exactly the same circumstances as in Monocotyledons, and exhibit precisely the same appearances (fig. 48). From this point, however, the further development

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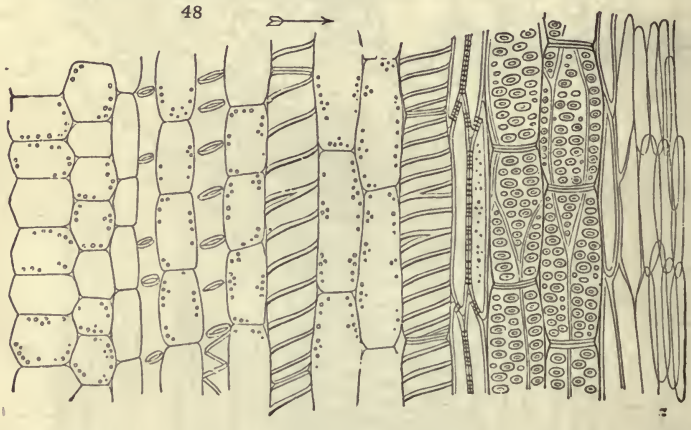

is very different, for here it is important to observe that all longitudinal extension of the parts of the plant ceases. When this takes place, the new-formed cells frequently continue to extend, so that they have not sufficient room; and the consequence is, that the ends of the cells in a horizontal layer press themselves between the ends of the cells which lie above them and below them, and thus they all become pointed. In all recently formed wood-cells it may be remarked that they are shorter than the old cells, and their ends are rounded. The peculiar form of the prosenchyma-cells is produced later. In the first part of the vascular bundles no such cells are ever found; the innermost are longitudinal parenchyma-cells, and pass gradually outwards into the wood-cells. But there are instances where no such extension of the recently formed cells ever takes place, and then the entire wood consists only of parenchymatous cells, as, for instance, in *Bombax pentandra*, *Carolinea minor*, and perhaps all *Bombaceæ*. In the later products of the formative activity of the cambium, a great difference in its growth is observed, according as the cells are developed as wood-cells (prosenchyma) or as they are uniformly or irregularly deposited. The simplest kinds of wood, on the one side, are those in which all the cells are similarly developed, and where no distinction between the cells and the so-called vessels exists. Such wood is seen in the *Coniferæ* and *Cycadaceæ*, consisting of lengthened prosenchyma, like broad cells with from one to eight rows of pores (fig. 49. *A*, *B*).

[48] Successive unclosed vascular bundles from *Vicia Faba*; a longitudinal section. The arrow denotes the direction from the pith to the bark. *a*, Cambium cells.

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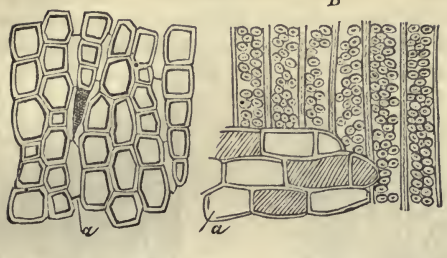


The wood of the species of *Mammillaria* differs little from this. At first sight it appears to consist of an entirely uniform tissue of somewhat extended cylindrical cells, which are distinguished by a most delicate spiral band projecting far into the cell (fig. 50. *B*). By greater observation upon longitudinal and transverse sections of the cells in which the spiral

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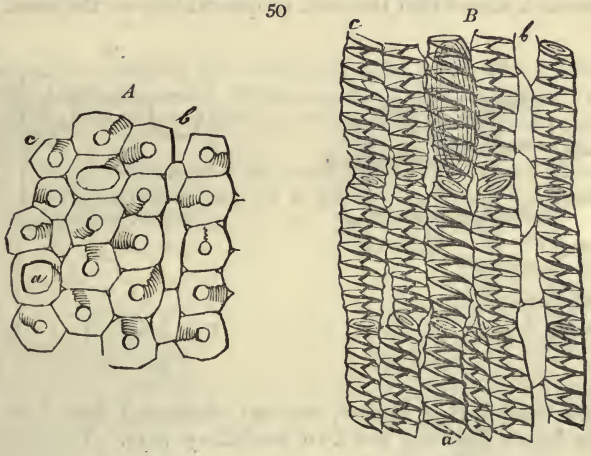


fibres project less into the cells, it will be found that they are in communication with one another, and allow air to pass through (fig. 50. *A a*, *B a*). This is the simplest form of the so-called vessel.

In another way a simple kind of wood is formed in *Carolinea minor*. It is extremely light and soft (like cork), and consists of regular parenchyma-cells, slightly elongated and somewhat porous, and of individual rows of much broader and longer, cylindrical, and clearly porous cells (called vessels), standing in open communication with one another. Very similar to this is the wood of *Bombax pentandra* (figs. 51, 52.), where we find, between the parenchymatous cells, individual, long, but tolerably thin-walled, prosenchyma-cells (figs. 51, 52. *b*). From this to the ordinary wood a transition is formed by some wood in my possession from the

[49] *A*, Transverse section of the wood of *Cycas revoluta*. *B*, Longitudinal section of the same, parallel to the medullary rays. *a*, In both figures, medullary ray cells. The most elongated cells have upon their walls innumerable large pores.

[50] *A*, Transverse section of the wood of *Mammillaria quadrispina*. *B*, Longitudinal section of the same, parallel to the bark. *a* and *c*, Spirally formed plates inside the cells: these cells contain only air. *b*, Medullary ray cells.

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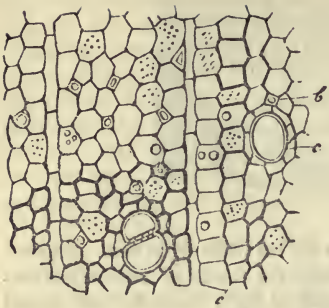


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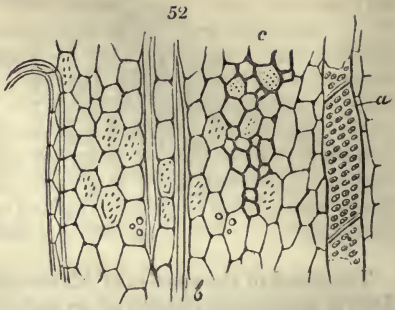


cover of a Chinese casket. At a cursory first glance the transverse section (fig. 53.) appears to exhibit clearly defined annual rings. More accurate research shows that the dark stripes which, as the most external

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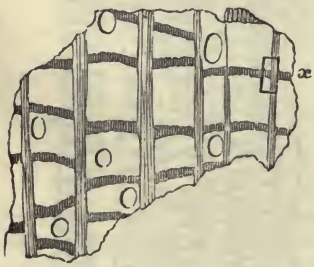


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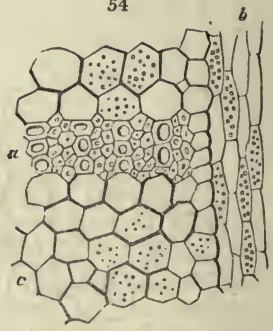


part of an annual ring, appear, are not connected, but form isolated transverse bands between the two medullary rays. These transverse

[51] Transverse section of the wood of *Bombax pentandra*. The entire wood consists of thin-walled but porous parenchyma (*c*), in which individual thick-walled wood-cells (*b*) are scattered. Small medullary rays, consisting of individual rows of cells, pass through the wood at pretty regular distances. In the under half of the section, the cell-walls become imperceptibly thicker, by which the boundaries of the two annual rings are clearly indicated. Single or in pairs, porous cells, lying on one another, pass through the wood (*c*).

[52] Longitudinal section of the same wood. *a*, Porous vessels. *b*, Wood-cells. *c*, Parenchyma.

[53] Transverse section of wood from a Chinese casket, with a low magnifying power. At first sight, the dark transverse bands might be regarded as the boundaries of the annual rings. They are not, however, connected together, and each extends between the medullary rays. The small space marked at *x* is strongly magnified at fig. 54., where it will be seen that the dark bands are formed out of small stripes of wood-cells, which alternate with a thin-walled porous parenchyma (*c*). Between the wood-cells and the medullary rays there exists also a layer of thin-walled parenchyma-cells. Between the wood-cells may be observed radial rows of somewhat broader and smaller thick-walled wood-cells. The thin-walled medullary ray cells (*b*) are also porous. Fig. 55. is a longitudinal section, parallel to the medullary rays; and the letters *a*, *b*, *c* indicate the same parts as in fig. 54. Large porous vessels are seen in fig. 53., which are not represented in the other figures.

bands consist exclusively of prosenchyma (figs. 54. *a*, 55. *a*), whilst the wood between which they lie consists of very regular, not much extended, thin-walled, and porous parenchyma (figs. 54. *c*, 55. *c*).

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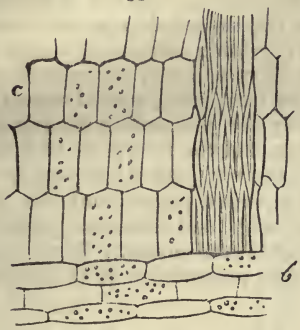


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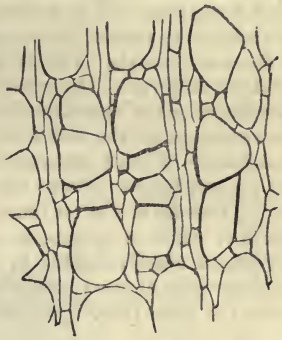

The opposite of this is the extremely light and porous wood of the various species of *Avicennia*, which consists almost entirely of very broad porous vessels, whose interstices are filled with small porous parenchyma-cells (fig. 56.).

Lastly, the great mass of most wood consists of longitudinal, thick-walled prosenchyma-cells, and, to a greater or less extent, of smaller porous vessels (figs. 57, 58.).

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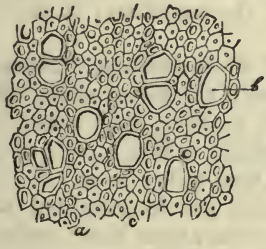


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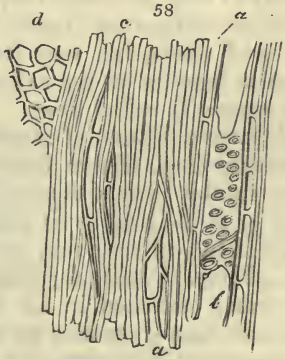



From the foregoing remarks and observations it will be seen that what are called vessels are unessential modifications of the cellular tissue, and care should be taken that no erroneous impression be conveyed by the once generally received term of "vascular bundles." Such bundles may

[56] Transverse section of the wood of *Avicennia*. The wood consists entirely of very broad porous vessels, together with very small thin-walled parenchymatous cells.

[57] Transverse section of the very heavy and thick wood of *Mahonia nepalensis*. The entire mass consists of very thick-walled wood-cells (*c*), and broad porous vessels (*b*). The cells of the medullary rays (*a*) are very thick-walled, and scarcely to be distinguished from the wood-cells.

[58] Longitudinal section of the same. *a*, *b*, *c*, correspond with fig. 55. *d*, the cut cells of a large medullary ray.

be seen without vessels in the longitudinal tissue of many *Cryptogamia*, as in the Mosses, also amongst the *Phanerogamia*, in *Mayaca fluviatilis*, some species of *Potamogeton*, in *Najas*, *Caulinia*, and *Ceratophyllum;* in short, in all plants growing under water, or which are nourished from their surface and not their roots. The term "vessel" has misled botanists, and it is time that we should be apprised of the fact that there is as much difference between the so-called vegetable vessels and those of animals, as there is between vegetable and animal wings and reproductive germs. The vessels of plants play but a very subordinate part in the functions of vegetable life, and, so far from being special organs for the circulation of the fluids of plants, they are themselves the last produced results of such movements of the sap, and the first parts to become filled up and impervious to the admission of the juices circulating in the plant. Vessels are often found wanting in entire plants, and the most important parts of plants, as in the gemmules and filaments, whilst in other plants closely related to these they are found present. These views of the doctrine of the vascular bundles I first propounded in Wiegmann's Archiv for 1839 (Bd. I. S. 220.).*

§ 27. *E.* Tissue of the Liber (*Tela fibrosa*, Bastgewebe). This is formed of cells so long that they cannot be regarded as cells superimposed upon one another, but as fibres lying close to one another. The walls of these cells are strong, often thickened so as to exclude the transmission of light, without exhibiting a clear configuration of the deposit layers. They are mostly soft and flexible. These cells seldom present themselves individually in the pith and the bark: they are more frequently seen in bundles (liber-bundles), in the visible nerves (veins) of flat small leaves, in the projecting angles of stems, and very frequently in the neighbourhood of the vascular bundles on the external side of the cambium; in the last it is especially called liber.

*F.* Liber Cells of *Apocynaceæ* and *Asclepiadaceæ*. These are peculiarly long, seldom branched cells, with thickened walls, which often exhibit very delicate spiral fibres crossing each other. In some spots their cavity is entirely obliterated, whilst in others they are swollen and vesicular, and contain a true milky juice.

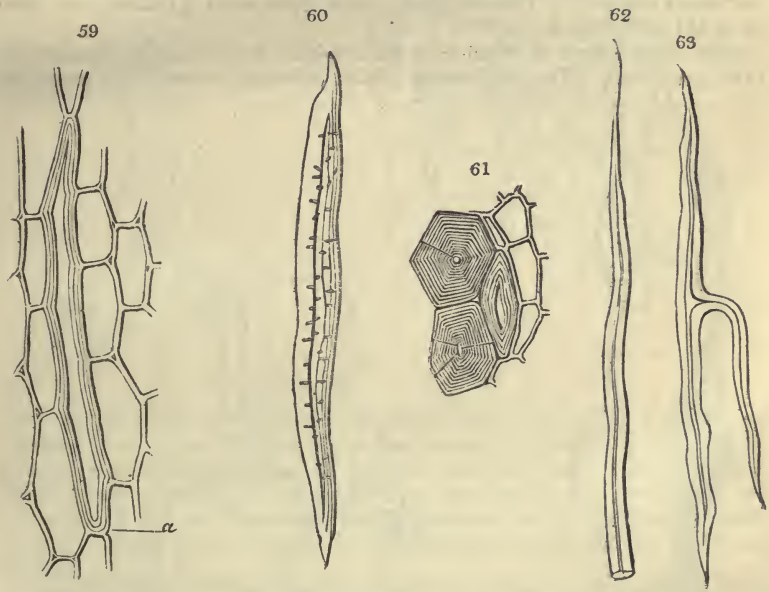
*G.* Milk Vessels (*Vasa lactescentia*), are longitudinal cells, frequently branched in all directions. Sometimes their walls are thin and homogeneous; at other times, especially from age, they are thickened by layers, and marked in a spiral manner (as in the leafless *Euphorbiaceæ*). They contain a colourless or variously coloured milky juice.

There are few departments of botany that offer more unanswered questions, and that demand greater research, than the subjects of the three preceding paragraphs.

The fibres of the liber in the youngest parts of the bud in which they can be seen are very short, almost spindle-shaped, cells, which lie with their sharp ends pushed between each other, so that as the part to which they belong increases in length, so do they increase also, but are brought

* This paper is also printed in Schleiden's Botanische Beiträge, vol. i. p. 29.; and has been translated in Taylor's Scientific Memoirs, and by the Sydenham Society.—Trans.

into closer contact, always pressing more and more upon each other, until they are quite parallel. They probably originate in parenchymatous cells, in the same way as prosenchyma. Between them and the longitudinal parenchymatous cells, there are a number of transition forms, and in many cases it is difficult to say to which form a particular tissue may belong. Such intermediate forms are very frequent in monocotyledons in the neighbourhood of vessels; they are also seen in dico-




tyledons, as in some of the *Cactaceæ* (fig. 59.). As they approach the character of shorter cells, the configuration of the walls, with pores or sharply defined layers, is evident (figs. 60, 61.).

If we regard the pointing at both ends and the thickness of the deposit layers as essential characters of liber-cells, then the branched cells discovered by me* in the ovary of some *Aroideæ* (in *Monstera* and *Scindapsus*), and in the pith of *Rhizophora Mangle* (fig. 63.), belong to them.

Ordinarily the liber-cells are so long, that the whole of them cannot be seen by a strong magnifying power (fig. 62.), and, next to the cells of some species of *Chara* and the pollen tubes of some plants, are the longest cells which present themselves in the vegetable kingdom. I have measured liber-cells from 4 to 5″ in length, but these are probably not the

* Wiegmann's Archiv, 1839, vol. i. p. 231.; Schleiden, Botanische Beiträge, vol. i. p. 42.

59 An intermediate form between liber- and parenchyma-cells (*a*), from the bark of the root of *Maxillaria atropurpurea*.

60 A liber-fibre, short, thick, and porous, from the *China regia*.

61 Transverse section of three liber-fibres and some parenchyma-cells from the *China regia* (*Cinchona scrobiculata* Humb. Yellow Bark.) The liber-cells show beautifully the deposit-layers and the porous canals.

62 Upper end of a liber-fibre from the *Tilia europæa*.

63 A branched liber-cell from the pith of *Rhizophora Mangle*.

longest. The branched liber-cells (fig. 63.), on account of their branching, are included in the following forms.

Upon the origin of the *liber-cells* of *Apocynaceæ* and *Asclepiadaceæ* no observations have been made: only thus much is certain, that they frequently contain milky juice. They are found singly, or in little bundles, near to, or in the place of, the liber-bundles; and are sometimes branched, *ex. gr.*, in *Hoya carnosa* (according to Meyen), and very beautiful in *Sarcostemma viminale*. The configuration of their walls is entirely the same as in old milk-vessels.

The *Milk-vessels*, in relation to their origin, have been at present but little examined. They appear at first as enlarged intercellular passages,

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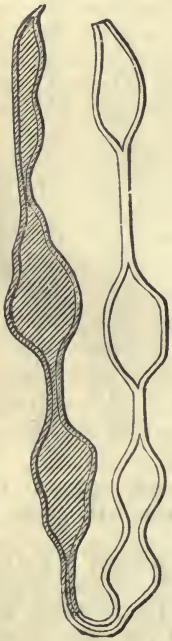

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and without any visible membrane (fig. 65.) to form them. Nor does any membrane appear to exist over the furrow formed by two neighbouring cells, as it does in all true cells. In old vessels, also, we often find impressions and projecting angles, showing that they must have fitted accurately into the surrounding cells (66. *A*, *B*). They are mostly branched in so compound a manner, that it is not often possible to examine a cell in its entire length (fig. 67.), yet it is easy to separate it into its parts if the tissue is treated with nitric acid. Without this means it is easily seen that they

[64] Intermediate formation between liber-cells and milk-vessels from the bark of *Ceropegia dichotoma*. The spiral stripes are drawn only in one half.

[65] Milk-vessels from the leaves of *Limnocharis Humboldti*. The walls of the upper part of the vessel at *a* are fallen together. The arrows show the direction of the currents. Every milk-vessel is enclosed by two rows of smaller and longer cells of parenchyma.

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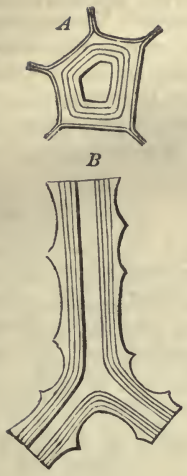


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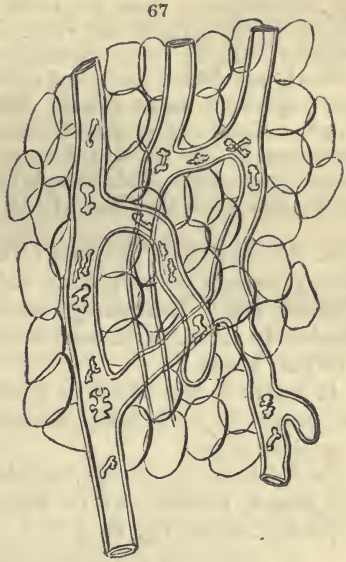

extend through the entire length of a plant, and often end in a *cul de sac*. This is so obvious in some forms of leafless *Euphorbiaceæ*, that it is wonderful how any difference of opinion could have existed on the point. In the older vessels, also seen well in the leafless *Euphorbiaceæ*, the spiral bands and the deposit-layers on the walls are easily distinguished, so that the lateral development of these organs agrees entirely with that of cells.

In their relation to one another, these three forms of tissue, as well as the receptacles of milk without proper walls, seem mutually to represent each other. They are seen before the vascular bundles of the stem, as receptacles of milk in *Mammillaria*, as liber in *Cereus*, as transitionary forms in the *Apocynaceæ* and *Asclepiadaceæ*, which in some species resemble liber-cells, whilst in others, as in *Sarcostemma viminale*, they are not to be distinguished from milk-vessels.

*History and Criticism.* — The liber and the milk vessels were known to the earliest observers. The proper walls of the last were first seen by Mirbel, but more accurately observed by Schultz, whose observations, overloaded by false theory and hasty inferences, have led to this principal result, that a large proportion of the milk-vessels do really possess a peculiar covering.* His theory of their origin, founded on insufficient observation, has become now quite antiquated. Unger

* Ueber Circulation des Saftes im Schöllkraut. Berlin, 1821. Natur der lebenden Pflanze. Berlin, 1832.

[66] *A*, A transverse section of a thickened milk-vessel from the bark of the stem of *Euphorbia cærulescens*, with the walls of the same lying upon the cells. *B*, A longitudinal section of the same, isolated through maceration. The sides of the vessel are irregular, from being pressed into the surrounding cells.

[67] Longitudinal section from the rind of *Euphorbia trigona*, parallel to the medullary rays. Many of the vessels branch and anastomose, whilst others end in blind extremities. Irregularly formed starch granules are seen in their interior.

thinks they originate from the union of rows of cells, but accurate observations do not support this view. Mirbel was the first to discover the liber-cells.* Meyen, in his Physiology of Plants (vol. i. p. 107.), appropriates to himself their discovery, but does not say where his observations on that subject are to be found. Mohl † first examined the liber-cells with care. Upon the origin of the liber-cells Meyen has set forth a peculiar view.‡ He believes them to originate in the union of rows of parenchymatous cells. This view is founded upon erroneous observations on the appearance of the liber-cells in the buds of *Æsculus*.

§ 28. *H.* Fibrous Tissue § (*Tela contexta*) consists of very long, thin, fibrilliform cells, intimately woven and variously mixed with each other. It is of two kinds.

*a.* It exists in the *Fungi* as a soft, almost sebaceous, and easily destructible cellular tissue.

*b.* In Lichens as a dry, tender, fibrous tissue, formed out of forked and branched cells (fig. 68.).

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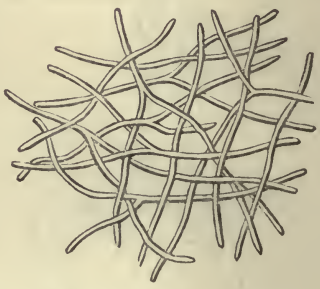

§ 29. *I.* Epidermal Tissue (*Tela epidermoidea*), is universally the most external layer of cells of a plant, so far as they can be distinguished from the cells they cover, by their form and contents. They only exist in the higher Cryptogamic and in nearly all the Phanerogamic plants.

It may be distinguished into,

*a. The Epidermis,* a continuous layer of cells, which may be again divided into three kinds, according to the medium in which it is developed.

1. *Epithelium.* Exceedingly delicate, homogeneous, transparent cells, filled with colourless juices, and covering the surface without forming intercellular passages. It is always present in the growing parts of plants, and remains longest in closed cavities, as in the ovary, but changes mostly into one or other of the following forms: —

2. *Epiblema,* consisting of compact cells flattened outwards, though not so at first, and without intercellular passages opening externally. They are developed in the water and in the earth.

3. *True Epidermis.* It consists of very flat tabular cells, whose walls laterally and outwardly are usually very compact. They are generally placed close to each other; but in most plants there

* Annales des Sciences Naturelles, 1835.

† Erläuterung meiner Ansicht über Structur der Pflanzensubstanz. Tübingen, 1836.

‡ Wiegmann's Archiv, 1839.

§ The English reader must not confound this with woody fibre, as this term has been sometimes thus used by British botanists. — Trans.

68 Fibrous tissue from the inner portion of *Cetraria islandica*, from a section parallel to its surface.

exists, at particular points, an intercellular passage, which, through the other intercellular passages and spaces, enables the subjacent parenchyma to communicate freely with the external air. At the inner opening of these intercellular passages, are placed (except in *Salvinia* and *Marchantia*) two semi-lunar parenchyma-cells, with their concave edges turned towards each other, which, according to the amount of their turgescence, allow a greater or less space to exist between them, or close the intercellular passage up altogether. These two cells, with the intercellular openings, are called stomates (*stoma*).

*b. Appendicular Organs.* They are all found upon the surface of plants, and are formed from cells. They are:

1. *Papillæ*, which are mere extensions of the external cell-wall, in the form of little elevations, as upon the petals of flowers; or as vesicles, as in *Mesembryanthemum crystallinum;* or as apparent hairs, as the so-called root-hairs.

2. *Hairs* (*Pili*) consist of one or more thin-walled cells, varied in their form and arrangement, and planted upon the epidermis. They are simple (*pili simplices*), branched (*p. ramosi*), stellate (*p. stellati*), scales (*lepides*), knobbed (*p. capitati*), glandular (*p. glanduliferi*) if the upper cells secrete a peculiar fluid.

3. *Setæ*, stiff, thick-walled, pricking cells.

4. *Stings* (*Pili urentes*) are stiff, thick-walled cells, terminating either in a point or a little head turned on one side, and mostly containing an irritating secretion. The cells at the base are often thin-walled, club-shaped, and swollen, and the whole enclosed by a number of wart-like cells produced from the epidermis.

5. *Thorns* (*Aculei*) consist of numerous rigid, thick-walled cells, firmly bound together, and terminating in a sharp point.

6. *Warts* (*Verrucæ*), formed out of many compact semicircular and variously formed cells.

*c. Cork* (*Suber*). In the cells of the epidermis there is often collected a grumous substance, from which are developed flat tabular cells. The epidermis bursts, and thus is formed what is popularly called "bark," or, where it is strongly developed and elastic, "cork," as in juicy fruits, but especially in the second year's stems of the *Quercus Suber*.

*d. Root Sheath* (*Velamen radicum*). In most tropical *Orchideæ*, and some *Aroideæ*, there exists upon the epidermis of the roots (the adventitious roots) a layer which is ordinarily composed of the most delicate cellular tissue, whose contents are entirely air.

The controversy about the nature of the epidermis was only possible at a time when the conception of the elementary structure of plants was of a very imperfect kind, and a false analogy with the epidermis of animals led to erroneous conclusions.

When a part is about to be formed from the cambium in phanerogamic plants, the first thing that meets our view is a layer of one or more series of delicate cells, which are homogeneous and contain a clear fluid,

and which form the external boundary and cover over the developing part. These cells of various signification I call *Epithelium* (fig. 69. *a*). The

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same thing may be observed in the so-called vascular cryptogamic plants (Ferns, *Lycopodiaceæ*, *Equisetaceæ*, *Rhizocarpeæ*). It is also seen in the *Marchantiaceæ*. This epithelium differs according to the external influences which act upon it. It is only in a few cases that the epithelium retains its true character for any length of time, as in the cavities of the ovary. In the air, in water, or in the earth, it becomes changed more or less, the cells become more compact, and their external surface flattened (fig. 70. *a*) in the air, so that most epidermis-cells have a tabular or ligulate form (fig. 71. *a*).

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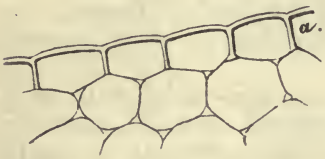


The forms which these tissues assume are very numerous. In the more delicate forms of these external coverings, as seen in the petals of some plants, individual cells elevate themselves above the surface (fig. 72. *a*), and thus form a transition to the simple forms of hairs.

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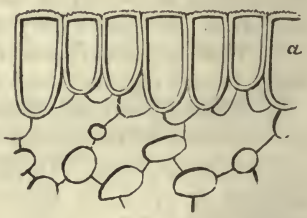


In other petals they are much more compact, and very much elongated from within outwards (fig. 73. *a*). The extreme of these two conditions occurs in the epidermis of some seeds, especially in those of the *Leguminosæ*. Here the cells are often long, cylindrical, extended from within outwards, and often entirely filled up at particular points (fig. 74. *a*).

[69] Epithelium (*a*) from the gemmules of *Tradescantia crassula*, with a layer of parenchyma-cells lying under it.

[70] Epiblema (*a*) from the root of *Spirodela polyrrhiza*, lying over a layer of parenchyma-cells.

[71] Epidermis (*a*) from the upper surface of the leaf of *Tradescantia discolor*, with the parenchyma beneath.

[72] Papillary epidermis (*a*) from the under surface of the petals of *Iris variegata*, accompanying the underlying parenchyma.

[73] Epidermis (*a*) of the under surface of the petals of the white rose. The external surface is beset with delicate furrows (*aciculatus*). Loose parenchyma underneath the epidermis.

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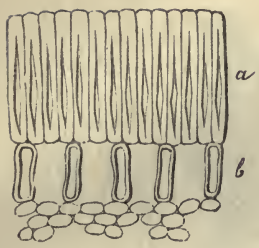


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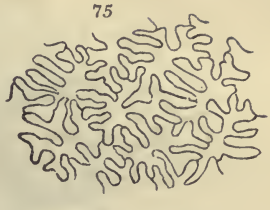

The gradual development of these external cells is attended with an irregular nourishment of their lateral walls, whereby round or pointed projections are formed, which are received into the concavities of the surrounding cells, so that a waving line appears. This causes a great variety in the appearance of the cells, according to the number of the individual cells, the size of the wavy bulgings, and the roundness or sharpness of their projections (fig. 75.). These cells are distinguished from those lying under them, by the presence of a transparent colourless or coloured fluid, but never, as has been erroneously stated, by containing air. The configuration of the cell-walls of the epidermis is very varied. A common phenomenon is, that their walls are, above and laterally, thicker than they are at the lower part, where they lie upon the parenchyma (figs. 68, 69.), as seen in the seeds of the *Asparagus officinalis.* Spiral formations abound in it, both with jelly in the seeds of *Hydrocharis Morsus ranæ*, and without jelly in the pericap of *Salvia verticillata.** The epidermis-cells are frequently porous, sometimes on the side where they touch each other, as in the leaves of *Epidendrum elongatum;* or where they touch the parenchyma-cells, as in the stem of *Melocactus;* they are least frequent externally, but this form presents itself in the leaves of *Abies.* In these leaves every one of the thick-walled external cells possesses three or four rows of porous canals, which run externally, and terminate in a small round cavity. The same thing is seen in *Cycas* (fig. 76.). The cells of the epithelium are placed so close to one another, that no intercellular passages are found opening between them. When epithelium is converted into epidermis in the air, it happens that the cells soften at their margins, and thus form inter-

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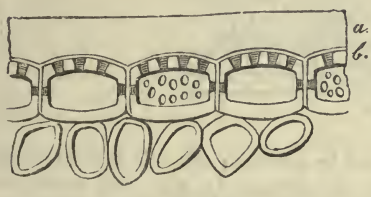


* Schleiden, Beiträge zur Phytogenesis, Müller's Archiv, 1838. See Taylor's Scientific Memoirs.

[74] Epidermis (*a*) of the seed of *Lupinus rivularis*, composed of long, very much thickened, cells. Under these is a layer of entirely separate cells, and beneath them parenchyma.

[75] Epidermis of the nectary of *Goldfussia anisophylla.* The cells are exceedingly flat and irregular. Section parallel with surface.

[76] Perpendicular section of the surface of a leaf of *Cycas revoluta.* The epidermis-cells (*b*) are laterally and externally porous. They are covered above by a layer of secreted matter (*a*).

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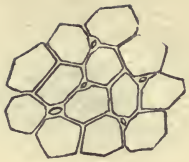

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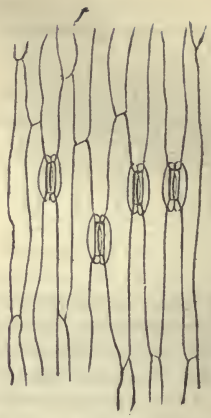


cellular passages, either generally, as in *Salvinia* (fig. 77.), or in particular spots, as in other plants (fig. 78.). Sometimes they occur in groups, whilst the remaining epidermis is free from intercellular passages, as in *Saxifraga sarmentosa;* and sometimes, in special, excavated pits, surrounded and concealed by hairs, as in *Nerium Oleander,* and species of *Banksia* and *Dryandra* (figs. 79, 80.). This intercellular passage during its growth is entirely

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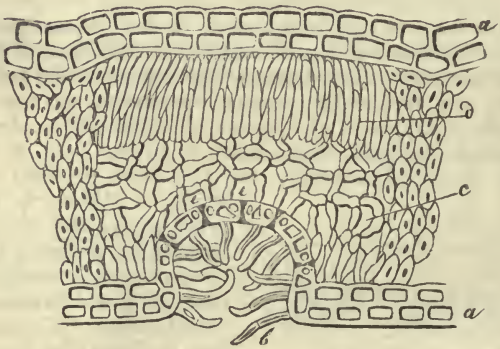


closed towards the inner part of the leaf by a simple cell. In the course of further development two new cells are formed in this cell, which is subsequently absorbed, and the two new cells gradually assume a semilunar form, the concave sides of which, being presented to each other, form an opening between them, through which a communication is

[77] Epidermis of the upper surface of the leaf of *Salvinia natans.* Here may be seen the simplest form of stomates, as intercellular passages between the epidermal cells.

[78] Epidermis peeled off from an *Allium,* with four stomates.

[79] Transverse section through the leaf of a *Banksia.* *a, a,* Epidermis, under which lies, on both sides, a layer of transparent cells. *c,* Spongy cellular tissue. *d,* Stretched cellular tissue of the upper half of the leaf; to the right and left, bundles of liber transversely cut through. *b,* A transverse section through one of the little pits of the under part of the leaf, which are clothed with hairs, and at whose base peculiar stomates (*e*) are found.

80

formed with the intercellular passage in the parenchyma. These semilunar cells are not found in *Salvinia*, nor in *Marchantiaceæ**, but are found doubled and trebled in some *Proteaceæ*.†

In the arrangement of the parts of these organs many varieties are found, especially in the relation of the stomatic cells with the intercellular passage, and the arrangement of the epidermal cells forming the inter-

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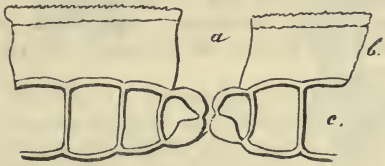


cellular passage; these peculiarities distinguish families and genera, as in the *Cactaceæ*, the Grasses, *Aloe*, *Tradescantia*, &c. The stomatic cells may be pushed somewhat outwards with their edges above the epidermal cells, or they may lie upon the same plane (fig. 81.), or they may lie entirely under the edge of the cells of the epidermis (fig. 82.). With regard to the second form here mentioned, we frequently see the cells lying next to the intercellular passage coloured differently, and

* In these plants the intercellular space ordinarily found under the stomates is beset with peculiar flask-shaped papillary cells.

† See Mohl, Ueber die Spaltöffnungen der Proteaceæ, in N. A. A. L. C. N. C. t. xvi. p. 2.

80 A parallel section of the under surface of the leaf of a *Banksia*, from which the epidermis is removed. *x*, The vascular bundles forming the network of the leaf. *a*, *b b*, Three little pits, which vary in appearance according as the section by which the epidermis was removed, cut deeply or superficially. The lower *b*, A pit with the hairs and stomates at the base: *a* exhibits the base of the pit, with the stomates; *b* exhibits the same, but the spongy cellular tissue is seen below. *c*, The epidermis clothing the base of the pit is removed, leaving nothing but the spongy cellular tissue.

81 Perpendicular section through the epidermal tissue of the leaf of a Stock. *c*, The epidermal cells covered with a layer of secretion (*b*), which, at the most external parts, is formed out of a more compact layer. *a*, Entrance to the stomate through the secreted layer.

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flatter, and the intercellular passage itself formed of a larger or smaller number of cells. In the *Marchantia* four cells are usually found ; in

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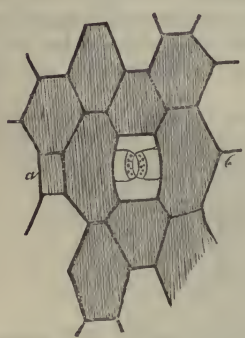


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*Cycas*, and at the base of the leaves of *Nelumbium* (fig. 85.), a much greater number. In most cases the epidermal cells lie on the same plane with the others, but in *Cycas* and *Marchantia* they are elevated so as to form a semicircular wart open at the point. In some instances a kind of stunting takes place, which, in the leaves of *Opuntiæ*, is almost normal. In this case, from three to five semi-lunar cells are pressed irregularly one upon another.

The contents of the stomatic cells, without exception, resemble those of the adjacent parenchyma, seldom or never those of the epidermal cells (figs. 83, 84.). I know of only a few cases, as *Agave lurida*, *Aloe nigri-*

[82] Perpendicular section of the surface of the leaf of *Hakea amplexifolia*. The stomate forms a large cavity, the bottom of which is closed on every side by two cells, which embrace between them the two special stomatic cells. The loose parenchyma contains many oddly-formed cells.

[83] Epidermis from the under surface of the leaves of *Tradescantia discolor*. The hatched cells contain a dark-red fluid. The two stomatic cells are surrounded by four regular cells, with perfectly clear contents.

[84] A perpendicular section of the surface of the above, in the direction *a*—*b*. The epidermal cells, filled with red sap, present a vacant space, which is closed externally by the flat clear cells, and the stomatic cells filled with chlorophyll.

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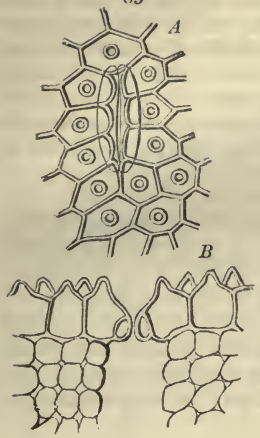


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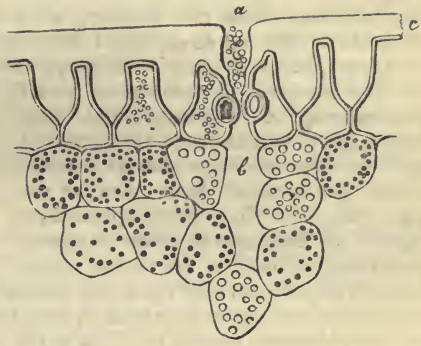


*cans* (fig. 86.), and some others, where remarkable substances, such as oil or resin, are present.

The epidermis of the roots of tropical *Orchideæ* and *Aroideæ* exhibit some very anomalous phenomena. In these cases the stomates lie upon the epidermis, and do not belong to the parenchyma of the bark, but to the root-sheath. The most regular and ordinary form of these internal stomates are seen in *Pothos crassinervis*, the most complicated and irregular in *Aerides odoratum*, and in various others they are more or less evident.

*History and Criticism.*—A knowledge of the functions and structure of the epidermal tissues depends upon accurate observation, which the author of this work was almost the only one to make during the present century. Much misunderstanding has, however, prevailed, and many bad observations have been made. The most important co-workers on this subject have been Krocker, father* and son†, Treviranus‡, Meyen§, Brongniart‖, Unger⊥, and Mohl¶. The view of Brongniart, that the epidermis is a delicate structureless membrane, will be mentioned presently (§ 69.). Recently, some botanists instead of using the term stomates have employed the expression skin-glands (Haut-drüsen), thus unneces-

* De Plantarum Epidermide. Halæ, 1800.
† De Plantarum Epidermide. Breslau, 1833.
‡ Beiträge zur Pflanzenphysiologie. Göttingen, 1811.
§ Phytotomie, s. 67. ‖ Annales des Sciences Nat. vol. xxi.
⊥ Die Exantheme der Pflanzen. Wien, 1833.
¶ Ueber die Spaltöffnungen der Proteaceæ, N. A. A. L. C. N. C. t. xvi. p. 2.

[85] Epidermis from the midst of the upper leaves of *Nelumbium speciosum*, with a stomate. The cells of the epidermis are elevated in the midst into a papilla, which, seen from the surface, appears like a ring. The stomate itself is formed of nine cells of epidermis, and under it lie two stomatic cells of the usual semilunar form. *B* is a perpendicular section of the same.

[86] A perpendicular section of the surface of the leaf of *Aloe nigricans*. *a*, Canal of the stomate, filled with orange-coloured granules of resin. *b*, Cavity under the stomate lined with cells, which contain granules of chlorophyll and resin. The papillose epidermal cells are filled with clear or dark-red sap, and rose-coloured granules of resin. Of the two stomatic cells, one contains chlorophyll, the other a large bright-yellow granule of resin. *c*, Secretion of the epidermis.

sarily playing with words. From a long series of researches I have come to the conclusion, that in at least two thirds of the whole vegetable kingdom the function of the two semi-lunar cells of stomates is no way different from the ordinary cells of the leaf. That in the other cases these cells act as glands, I do not at all believe.

*Appendicular Organs.*—Although the epidermal cells are universally the first in which the process of growth ceases, yet it often continues in particular spots. The most simple form is the mere extension of the external cell-wall into longer or shorter papillæ, which give to petals their peculiar aspect, and roots their hairy appearance (fig 87.). Frequently these papillary growths exist only at particular spots, and the papillæ develop from two to five cells, which at first are round, but afterwards become extended, and thus form a cellular upright hair of the epidermis (fig. 88.). This is the general way in which hairs are

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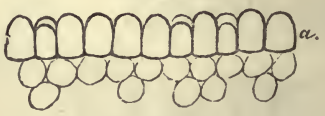


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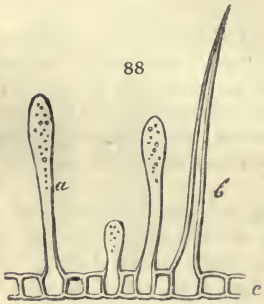


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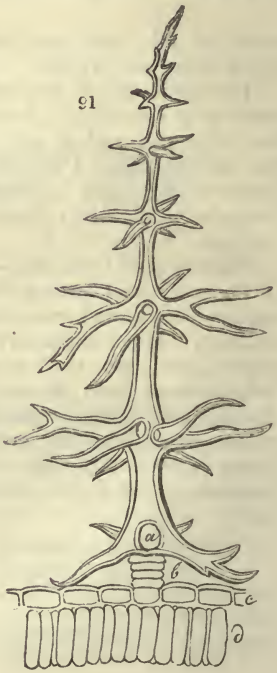


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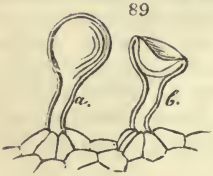


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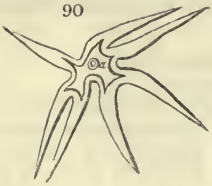



[87] Papillary epidermis from the under surface of the petals of *Iris variegata*, with underlying cells of parenchyma.

[88] *c*, Epidermis, with simple hairs, from the stem of an *Œnothera*. *a*, Club-shaped hair. *b*, Pointed hair.

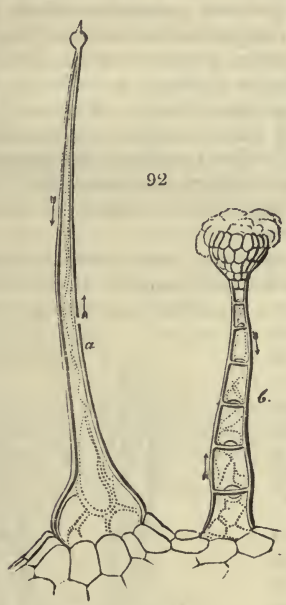
[89] Part of the epidermis of the leaf of *Helleborus fœtidus*, with two hairs. Every hair (*a*) is swollen and club-shaped above, and appears to contain a poisonous secretion. The hair becomes gradually empty, and falls in, as seen at *b*.

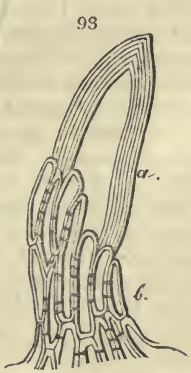
[90] Stellate hair of *Alyssum rostratum*. *a*, Its point of attachment.

[91] *c*, Epidermis, and *d*, the parenchyma, of *Alternanthera axillaris*, with a single hair. This consists of a series of flat cells at the base (*b*), and a multiform thick-walled cell above. *a*, Spot where a branch of the cell has been removed.

developed, but further special researches are needed. Frequently a hair consisting of a single cell is developed into manifold forms, sometimes swelling into a knot (figs. 88, 89.); at other times forming numerous branches (fig. 90.), as, for instance, in the hairs of some species of *Malpighia* and *Rhamnus*, in which the branches of the hair extend in two opposite directions, and are pressed flat upon the surface of the epidermis; and also in the remarkable four-armed pair of cells in the vessels of *Utricularia*. These at first consist of two round cells lying close to one another; they then form two short pedicels, which swell and form a little head, each of which sends out two arms, a long one and a short one.

In most cases, several cells go to form a hair. In this case the branches often consist of cells (fig. 91.). Amongst compound hairs those bearing knobs are very frequent. The pedicel either consists of a single cell, or a row of cells (fig. 92. *b*), or several cells. The same




thing occurs in the structure of the knob, which is often green, or coloured, or contains a peculiar secretion.* Sometimes hairs exhibit in the interior spiral vessels, as in *Drosera*. The most remarkable

* I cannot entertain the notion of a gland in the vegetable kingdom; so that here, as elsewhere, I make no distinction.

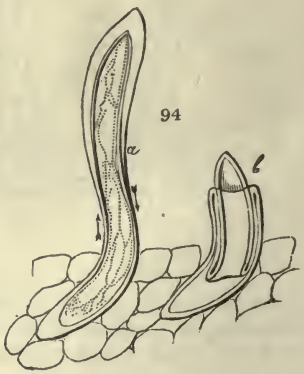
[92] Lateral view of a portion of the epidermis of the *Wigandia urens*, with two hairs: *a* is a stinging hair, with a knob, and circulating fluid in the interior; *b*. a club-shaped glandular hair. Every one of the simple cylindrical cells, which, placed one upon the other, form the stalk, exhibit a cytoblast and circulation. The knob, formed out of many little cells, is covered with secreted resin. The arrows show the direction of the streams.

[93] A prickle-hair from the leaf of *Dipsacus fullonum*. It consists of a long, somewhat bent cell, thickened by layers (*a*), which is embraced at the base by an elevated mass of porous epidermis-cells.

of the epidermal processes are the stinging hairs. They constitute the type of a very common form of the epidermal tissue, in which a few wart-like cells are elevated above the surface, and embrace the base of a single elongated cell (figs. 92, 93. *a*).

Such hairs, very much thickened and distinguished by the porosity of the epidermal cells, are seen in *Dipsacus* (fig. 93.); ordinarily the lower cells of such hairs are swollen, with thin walls, whilst those above are pointed and thick-walled. They are frequently marked on the upper surface with little warts spirally arranged, and with elevated stripes. This form characterises the *Urticaceæ*, the *Boraginaceæ*, the *Cucurbitaceæ*, and the *Loasaceæ*. The mechanism also of the stinging hairs in *Urtica*, *Wigandia urens*, and the *Loasaceæ*, is very interesting. Almost all stinging hairs end in a little knob-shaped swelling, which is exceedingly brittle, and easily knocked off by a touch. The opened point, on being pressed against, exudes the secretions contained in the cells at the base of the hair, and will produce poisonous effects when introduced into animal tissues. Our indigenous nettles are the least injurious. The stings of the *Loasaceæ* are much more so, while the *Urtica crenata* and *crenulata* of the East Indies produce wounds in which pain is felt for weeks and months after touching them. The most dangerous of all is the *Urtica urentissima* of Blume, called in Timor *Daoun setan*, and by the English "Devil's leaf." The wounds of this plant give pain for years after, especially in damp weather, and occasionally death from tetanus is the result. Could we separate this poison, it would be the most powerful vegetable poison known.

In the early stages of growth these hairs, all of them, possess an active circulation of the sap. Some hairs have their contents absorbed at a special time, so that the hair is, as it were, absorbed into its own proper cavity. This remarkable phenomenon takes place in the hairs of the style in *Campanulaceæ** (fig. 94.). Also in the globular cells of knob-shaped hairs, which then look as if half had been cut through, or as if a cover had been removed.† Meyen has published a work on hairs, distinguished by a host of peculiarities.‡




*Cork.*— A peculiar change goes on in the epidermal cells of particular parts, more especially the stem and fruits of certain trees. A quantity of yellow slimy matter collects in the cells and gradually increases in quantity, so that the external cell-wall is torn by the under one and lifted above the surface. Cells are formed in a hitherto undiscovered manner in the yellow substance, which assume the form of four-cornered tables, and are arranged in connected concentric layers. When perfectly formed, this

* See Brongniart, Ann. de Sc. Nat., 1839, p. 244.
† According to Meyen; but it is erroneous.
‡ Ueber die Secretionsorgane der Pflanzen. Berlin, 1837.

[94] Longitudinal section through the style of a *Campanula*, with two hairs: *a*, a hair exhibiting a circulation; its point is enclosed in a layer of mucus: *b* has lost its contents, and is in consequence contracted.

tissue exhibits great elasticity, and the tissue known by the name of cork belongs to this form. It exists, however, in countless other forms, and its existence seems detetermined by the presence of an epidermis which vegetates for a longer period than is usual. When the process of cork-formation once commences, it goes on; but should the layer be thrown off the tree at any particular stage of its growth, it is not again engendered, as, for instance, in the vine and the *Clematis Vitalba.* Mohl * was the first who accurately examined this subject, and I have sought to explain its origin. †

*Root-sheaths.*—If the organs of *Pothos crassinervis*, called aërial-roots, are examined, there will be found a distinct epidermis, with stomates whose semilunar cells, filled with a brown granular matter, are elevated above the surface of the epidermis, and form a special tissue whose walls exhibit the most delicate spiral fibres. These cells are filled with air, and thus give the brilliant white appearance to these roots. How this layer originates is not very clear, but it is formed in the same way at the points of the roots as in the other parts. The same layer is found on the roots of most tropical *Orchidaceæ*, and the cell-walls exhibit in them the most striking modifications. It is very remarkable in *Aërides odoratum.* I have seen it in *Epidendrum elongatum, Cattleya Forbesii, Brassavola cordata, Maxillaria atropurpurea, M. Harrisonii, Acropera Loddigesii, Cyrtopodium speciosissimum, Oncidium altissimum*, and other species. I also found it, but without spiral fibres, in *Pothos reflexa, acaulis, violacea, cordata, longifolia*, and *digitata.* In other families I have not seen it. The roots have ordinarily a fresh green point; in these the cells are full of sap, and the green cortical parenchyma is seen through them. The relations of this layer differ so much from those of the epidermal cells, that it has been regarded as a peculiar tissue. Link ‡ first discovered this layer, Meyen § examined it more accurately, but no one has correctly appreciated it.

* Ueber die Entwickelung des Korkes und der Borke. Tüb. 1836.

† Beiträge zur Anatomie und Physiologie der Cacteen.

‡ Elem. Phil. Bot. Ed. i. p. 393.

§ Physiologie, i. p. 47. Meyen, copying Link, says that Dutrochet has examined this tissue; but this is a mistake.

# CHAPTER II.

## ON THE LIFE OF THE PLANT-CELL.

## SECTION I.

### FUNCTIONS OF THE INDIVIDUAL CELL.

§ 30. ALL the chemical and physical powers of the earth naturally act upon the plant-cell. Inasmuch as these striking phenomena are called forth, and especially as they exhibit, in and through the cell itself, an especial form of action, I call all such action the life (*vita*) of the cell. Most of the physical powers of nature are too little known for us to be able to comprehend the peculiarities which they exhibit under especial relations. We can only say generally that the various chemical processes which take place in the cell must be accompanied by changes of temperature, electricity, absolute and specific gravity, &c., without being able to count or measure the same. There are, therefore, only a few relations which permit of a more accurate estimation, as the absorption of foreign agents (*endosmosis*), the decomposition and recomposition of the same (assimilation and secretion), the getting rid of superfluous matter (exhalation and excretion), the working up of the assimilated matter (organisation), the movements of the contents of the cell (circulation), the movement of the whole cell (locomotion), the formation of new cells within the old ones (propagation), and the cessation of all these processes (death).

### I. *On the Absorption of Foreign Agents.*

§ 31. The cell-membrane (in its young state) is perfectly closed, but permeable to all fluids. It thus takes up all perfect solutions through its walls into its cavity. In consequence of the chemical change going on in its interior, the cell constantly contains a fluid thicker than water, or dilute solutions of saline substances, and mostly one which, like a solution of sugar or gum, has so great an affinity for water, that they draw water into the cavity with a certain degree of force, and, on the other hand, a small quantity of the concentrated fluid passes out of the cell. The passing in of the fluid into the cell has been called by Dutrochet endosmose, and its passing out exosmose.

The property which cellulose possesses of allowing fluids to pass through it has already been mentioned. It is an entirely superfluous

and gratuitous hypothesis to suppose that it possesses invisible pores, or that the membrane stands in the same relation to fluid as salts to water. In the latter case, the water is supposed to dissolve up a little of the membrane, which, in passing through, it yields up again. The passing of the fluid through the membrane is produced by the relation of water to certain other substances contained in the cell. If gum or sugar is dissolved in a small quantity of water, and pure water is poured carefully over the solution, the two liquids remain apparently for a short time unmixed, but at the edges where the fluids meet a process goes on, in which the two fluids pass one into the other until the whole is completely mixed. If the two fluids are separated by a vegetable or animal membrane, the attraction is not diminished, because both fluids penetrate the membrane and thus come in contact, but the thicker fluid passes through the membrane with more difficulty than the thinner. Thus a larger quantity of the thin fluid, in the same time, is found present with the thicker than of the thicker with the thinner. The experiment may be performed in glass tubes, when the relative height to which the fluids will rise in a given time will be in proportion to their relative thickness. The same results take place when fluids, not thickened, but varying in specific gravity, as alcohol and water, are employed, the lighter passing into the heavier most rapidly. Dutrochet called the passing in of the thinner fluid endosmose, and the passing out of the thicker exosmose, and measured the endosmotic power of the fluids by the difference of height which they reached in tubes. By means of a graduated apparatus, Dutrochet estimated the relative power of the following substances as compared with water: —

| | | |
|---|---|---|
| Animal albumen . . | at | 12 |
| Sugar . . . . | | 11 |
| Gum . . . . | | 5·17. |

Vegetable albumen belongs to the nitrogenous vegetable substances, and is similar in many points to animal albumen. In its physical properties it is difficult, if not impossible, to separate it from the vegetable substance described above as mucus (protein). It appears to me not too much to assume that this vegetable albumen (mucus), out of which the cytoblast is formed, possesses the same endosmotic power as animal albumen. We can thus easily explain how it is that, immediately after the cytoblast is surrounded by a membrane, endosmose begins, and thus takes up those substances upon which the cytoblast exercises a changing influence. In this way sugar and gum are formed, and the cell is thus filled with substances which increase the process of endosmose. Scarcely any further explanation of the process of absorption is needed, as this simple process suffices for the understanding the most complicated phenomena of vegetable life.

It is to be regretted that so few experiments have been made on the relations exhibited by this process. There are two points of especial importance. The first is, the great variety in the nature of the various substances within and without the cells of plants, and the great difference in the power with which they are attracted: on the relation of numerous solutions to one another, we have no experiments. In the second place, the nature of the separating membrane demands attention. Water and alcohol, for instance, exhibit a very powerful reciprocal attraction; but in an endosmotic apparatus, when bladder or caoutchouc is used as a means of separation, the result is very different. With the bladder the water passes to the alcohol, but not *vice versâ*, as alcohol does not easily permeate animal membrane. With the caoutchouc the result is exactly the

reverse, the alcohol readily passing through this substance. Similar modifications in the simplest processes of cell-life must take place, on account of the countless varieties of cell-membrane. In all experiments, however, it is necessary to avoid the the hypothesis of the porosity of the organic membrane, which can only be attended with the same bad results as the notion of the existence of atoms in chemistry.*

§ 32. The most universally distributed medium of solution in nature, water, is also the fluid which is absorbed by the plant-cell, and conveys all other matters into its interior. The most essential of these matters are carbonic acid and ammonia, both of which are contained in water which either falls from the air or has been a long time in contact with it. Water, carbonic acid, and ammonia contain carbon, hydrogen, oxygen, and nitrogen, all of which are essential to the formation of the assimilated substances and to the especial nourishment of the cell. But the water occasionally conveys to the cell, in small quantities, all substances which are capable of solution in water.

In spite of the almost endless works upon the nourishment of plants, nothing is in a more uncertain state than our knowledge of the food necessary for plants. This has arisen from the facts having been selected from, and the experiments made upon, the higher and more complicated forms of plants instead of the lowest. The simplest and most natural object for such researches is the *Protococcus viridis*, or some other simple *Conferva*, which consists of one or only a few cells, and which floats free in water, and contains the substances universally necessary for the life of the cell. These plants require nothing more for their vegetation than pure water, which has taken up from the atmosphere carbonic acid and ammonia, and perhaps a very small quantity of inorganic salts; the necessity for which last has not been proved, but is supposed to be necessary from analogy with the higher plants. The experiment is easily made of supplying these plants with water containing a large quantity of carbonic acid, when they will be found to grow more rapidly, and thrive more luxuriously, than when placed in water to which humus, humic acid, or humic acid salts have been added. This is sufficient proof that these last substances are not essential to the life of the cell.

It is worthy of remark, that just as *Carices*, and other so-called moor-plants, flourish with a certain quantity of humic acid, which is generally unfavourable to vegetation, so also other plants, as the little *Conferva* which requires tannin and grows in infusions of galls, require other substances. The *Mycoderma aceti* grows under the influence of the decomposition of vinegar. In these cases, probably, the free acid is as little necessary to nutrition as in other plants, but the mode and manner of the decomposition of the acid is a favouring moment for the vegetation of the above-named plants.

Few researches have been made on the nature of the nitrogenous substances in the simplest plants. I have hitherto supposed that the nitrogenous compounds of plants are pure protein. But if we regard

* See Dutrochet, L'Agent immédiat du Mouvement vital dévoilé, &c. Paris, 1826. Also Poggendorff's Annalen, vol. xi. p. 138., vol. xxviii. p. 134.; and Schweigger's Journal, lviii. p. 1. 20. [Also Draper on the Chemistry of Plants, and Matteucci on the Physical Phenomena of Living Beings.—Trans.]

them as albumen, fibrin, and casein, we must allow for the absorption of sulphur and phosphorus, as well as salts of sulphuric and phosphoric acids: through this the phenomena become much more complicated. The reduction of the phosphates and sulphates to phosphoric and sulphuric acids, and the separation of the sulphur or phosphorus and the oxygen, indicate complicated chemical processes, which are not, however, performed without the presence of nitrogenous substances, and thus they appear to be the simplest additions to the plant-cell next the formation of protein. The notion of such changes is justified by Mulder's researches upon the mother of vinegar (*Mycoderma* Pers.), which is formed out of hydrated acetic acid and the albumen contained in the vinegar. It is composed of cellulose and protein, which always exist in the proportion of one equivalent of protein with four of cellulose.* A similar accurate examination of the fermentation-cells would be of the highest interest.

The plant-cell takes up all substances that are in solution in water, both mineral and vegetable poisons and tannin, which, by producing an interruption of the chemical processes, are capable of destroying its life. The cell in this view has no choice beyond the endosmotic power of the various substances which are presented to it.† On the other hand, every fluid is unfit for the nutrition of the cell, which, on account of its specific nature as alcohol, or its density as concentrated solutions of sugar and gum‡, renders endosmose impossible, should it even contain all the elements necessary for the growth of the cell.§

In the last place we may observe, that in the changes which are undergone in the cell of the plant there is no individual element, with the exception of oxygen, which takes part alone in those chemical processes. Nitrogen is taken in with water, but passes out again without undergoing any change. Hence all calculations with regard to the composition and metamorphoses of organic bodies, in which the pure elements, and not their combinations, are supposed to play a part, must be rejected as hypothetical.

## II. *On the Assimilation of the absorbed Matters, and Secretion.*

§ 33. The assimilated substances consist of carbon, hydrogen, oxygen, and nitrogen (sometimes with sulphur and phosphorus); and these are only assimilated from the definite combinations, carbonic acid, water, and ammonia. As soon as these substances are conducted into the interior of the cell, in the before-mentioned manner, chemical processes originate which first commence in the destruction of the ammoniacal compounds and (perhaps as a result) the decomposition of the water, and whose progress is distinguished by the action of the assimilated nitrogenous matter (mucus) upon non-nitrogenous substances. Thus are formed at the same time both mucus and non-nitrogenous substances.

* Liebig's Annalen, vol. xlvi. p. 207.

† See the experiments of Saussure, Chemische Untersuchungen über die Vegetation, Leipzig, 1805, p. 228.

‡ De Saussure and Davy found that plants flourished on dilute solutions of gum and sugar.

§ Davy, Elements of Agriculture.

I call those assimilated matters which have been mentioned above in the chapter on the substances contained in plants. We can only place in this class those substances which are produced and exist in the simplest cells, and which are necessary universally for the growth of the plant-cell. I do not say that those mentioned above are all, as subsequent researches may add to their number by the discovery of unsuspected relations. There is, for instance, resin, which, though frequently present, is excluded because we cannot detect its transitions to the assimilated matters as we can in the fixed oils. In this way we may draw a permanent and useful distinction between assimilated substances and secretions. I would, however, disclaim here any analogy that may be supposed to exist between these substances and those of the animal kingdom, and must insist on regarding these terms as connected with ideas belonging to the vegetable kingdom alone.

There can be little doubt that all the foregoing processes of decomposition and recomposition of the substances of which the plant-cell is composed have their foundation in well-known chemical powers and laws. That the elements of which the plant-cell is composed obey the same laws in the cell as out of it, seems warranted by the strongest presumptions of inductive inquiry. All the elements of which plants are composed are derived from the inorganic world, and the combinations which carbon, hydrogen, oxygen, nitrogen, &c. enter into in the plant take place under the influence of the properties or powers which they possess independent of the plant-cell. It is for those who suppose that these substances undergo some change in passing into the organism to bring forward some proof of such a change. So long as this proof is wanting (and it ever will be), we must regard it as true that all the chemical laws find uncontrolled exercise in the organism. The activity of the modern school of chemists, Liebig and his followers, Dumas, Mulder, &c., lead us from another point of view to the same results. Their labours have placed the perfect identity of the elements and processes which go on in and out of the body upon the most satisfactory inductive basis. Liebig and Mulder especially have shown that, if we analyse the course of changes which occur in the elements composing an organism according to the laws of inorganic chemistry, we come to the same results as though they were independent of the organic body.

The questions to be solved in this department of vegetable physiology are, first, what are the compounds, and what the chemical processes, by which the simplest plant-cells are formed; and, secondly, what are the compounds, and in what way are formed the substances, which are contained in every plant-cell. For a knowledge of the compounds, ammonia, carbonic acid gas, and water, which are every where and universally required for the formation of the assimilated matters, we are indebted to the chemists, De Saussure, Liebig, and others. Liebig * has rightly exposed the absurdity of those who attempt to explain all organic phenomena by what takes place in the elements, away from an organism. There is, however, one fact which occurs in inorganic bodies which exercises the most important influence in organic combinations. It is, that bodies will enter much more freely into union with each other at the moment they are released from other combinations than at any other time. A body in this condition is said to be *in statu nascenti*, in a nascent state. Of the substances which constitute the food of plants,

* Chemistry in its relation to Physiology and Pathology.

two, water and the salts of ammonia, easily enter into a state of decomposition. Water on coming in contact with zinc gives off its hydrogen, and the weakest galvanic current serves to separate its oxygen and hydrogen; whilst an alteration of temperature or solution is sufficient to decompose or produce important alterations in the salts of ammonia. Thus, through the destruction of a single equivalent of water, an impulse would be given to an endless chain of chemical processes, which would result in the development of those substances which are found in the plant-cell. The question is, however, still unanswered as to what change is the first that takes place in the series. Liebig has observed, very correctly, that, as far as the ultimate results are concerned, it signifies little whether carbonic acid or water is first decomposed. Although, as before stated, we must not explain the changes which take place in the cell on the supposition that the elements, as such, unite together, yet, on the other hand, we are not in a position to say that the formation of starch, &c. is dependent on the decomposition of carbonic acid and water. Where plants grow, and where cells are formed, there we have present at the same time water, carbonic acid, and the compounds of ammonia. We also see that nitrogenous and non-nitrogenous substances are developed at the same time, and apparently by the same process. In this point of view, the analogy between the composition of vinegar and the mother of vinegar, which last, according to Mulder, consists of one equivalent of protein and four equivalents of cellulose, is a matter of some interest. Thus:

| | C | H | O | N |
|---|---|---|---|---|
| 74 Water (H O) = . . | — | 74 | 74 | — |
| 94 Carbonic acid ($C O^2$) = . | 94 | — | 188 | — |
| 2 Carbonate of ammonia ($H^2 N^6 CO^2)^2$ = | 2 | 2 | 4 | 12 |
| | 96 | 76 | 266 | 12 |
| Forms | | | | |
| 1 Protein = . . | 48 | 36 | 14 | 12 |
| 4 Cellulose ($C_{12} H_{10} O_{10}$) = | 48 | 40 | 40 | — |
| 212 Oxygen = . . | — | — | 212 | — |
| | 96 | 76 | 266 | 12 |

The 212 of oxygen would suffice to convert 53 equivalents of alcohol into acetic acid.

But if we leave out of the question the nitrogenous substances, the following scheme will give us the changes that occur in carbonic acid and water:

| | C | H | O | |
|---|---|---|---|---|
| 12 Carbonic acid = . . | 12 | — | 24 | |
| 24 Water = . . | — | 24 | 24 | |
| | 12 | 24 | 48 | |
| 24 O = . . | — | — | 24 | |
| X = . . | 12 | 24 | 24 | |
| X = 1 Grape Sugar + 12 Water = | 12 | 12 | 12 | + 12 H O |
| or 1 {Cellulose, Dextrin, Cane Sugar, Inulin} + 14 „ = | 12 | 10 | 10 | + 14 H O |
| „ 1 Wood (Prout) + 16 „ = | 12 | 8 | 8 | + 16 H O |

These changes require no further explanation than the decomposition of water, the setting free of oxygen, and the separation of a smaller or larger number of equivalents of water; processes which we know constantly present themselves in the decomposition of organic substances.

One of the most important of the proximate principles is undoubtedly dextrin. In all formative fluids, according to Mitscherlich and Mulder, dextrin presents itself as the primary substance out of which all the other assimilated matters are formed. In the various changes which these matters undergo, the nitrogenous bodies seem to be the means of effecting changes in the other bodies, whilst they themselves remain unchanged. This phenomenon has got various names without any explanation of it being given. Berzelius calls the process catalysis; Mitscherlich, the contact of substances; and Liebig the activity of apprehending bodies. A number of such chemical facts are known; thus — sulphuric acid, with heat, converts starch into dextrin and sugar and alcohol into ether; diastase changes starch into dextrin and sugar; albumen, protein, &c. convert sugar into alcohol. Liebig's explanation of the phenomenon as a communication of motion is founded on the notion of the existence of ultimate atoms, and is otherwise untenable. Could we explain better this phenomenon of one of the assimilated substances facilitating the changes which go on in the others, we should have yet to explain the changes which produced the nitrogenous substances.

The most important of these changes appears to be the decomposition of water, but we are at a loss to know whose calculations to adopt. Almost all plants need for their growth the influence of light. Here also we have a need of experiments to determine the action of the particular rays of the sun-light, as of the coloured, the calorific, and the chemical. Only thus much is known from De Saussure's experiments: that under the influence of light the carbonic acid of the air is fixed in the cells, and combines also with hydrogen; a process which will not go on when light is excluded. That in this case light can be supplied through hydrogen, appears to be proved by an interesting experiment of Humboldt's.*

§ 34. In the formation of the assimilated matters, many substances become free, which, either through their natural affinities, or the effect of contact, or predisposing affinity, form new combinations either amongst themselves, or with the non-assimilable substances which may have been absorbed at the same time. All substances formed in this way I call secretions (*materia secreta*) of the cells. Some of these are universally present, as free oxygen, or at least when they have vegetated under definite circumstances, as the green colouring matter (chlorophyll). There are others whose formation depends on especial circumstances, as conia, solania, and the like. The chemical changes by which such substances are produced are for the most part concealed. Two points remain to be noticed here: — 1. That these secretions would be frequently injurious to the cells were they not neutralised by inorganic substances taken up from without or by newly formed organic matters: thus, oxalic acid combines with lime, and the

* Floræ Fribergensis Specimen, p. 180. [See also, on this subject, Hunt's Reports in the Transactions of the British Association, 1847; and Draper on the Chemistry of Plants.—Trans.]

alkaloids are found united to the organic acids. 2. Bodies such as tannin, resin, &c., are frequently formed which have a great affinity for oxygen, and thus from the vicinity of the cell absorb a considerable quantity of this gas.

There is more need perhaps of research on these subjects than those of preceding paragraphs, but yet sufficient is known to impress us with the fact that all depend on physico-chemical processes. The great insecurity here arises from the deficient knowledge we possess of the relation of these substances to the so-called indifferent bodies. We know that starch, sugar, &c. are composed of so many atoms of carbon and water, but not how they are actually formed, or how they originate from their elements.

Above I have divided the secretions from the assimilated matters; and though some of the former should ultimately be placed among the latter, it will not affect the propriety of this division. We might here classify these secretions according to their greater or less extension throughout the vegetable kingdom; but such an arrangement would have no relation to the processes of life in the plant-cell, and therefore would be superfluous in this place.

Two points must be noticed here. The cells take up with the water various salts. A part of them are inorganic, a part organic. Of the first a part, perhaps, remain in the cell from the evaporation of the water. Another part are decomposed in manifold ways through the chemical processes which go on in the inside of the cell. From these are produced new bodies, which again decompose each other, and act upon those bodies already formed; and thus the whole of the processes become more complicated. A part of the salts seem also destined for the neutralisation and removal of the acids produced by necessary processes. The presence of a large quantity of oxalate of lime in the *Cactaceæ* is thus explained, the injurious oxalic acid which is formed in the cell being united to lime, which is taken up from without in the form of a soluble carbonate of lime, and an insoluble and innocuous salt is thus formed. Liebig* has given an opinion that a certain quantity of bases appear to be constant, in every plant, in every locality. Perhaps, they are those which the plant cannot do without to bring its chemical processes into equilibrium. A similar equilibrium may be found between some of the substances which are injurious, and formed in the cell, and which united together form perfectly harmless bodies.

The substances which are formed in the cell, and which have a great affinity for oxygen gas, will take up this substance from without the cell, provided it is not supplied them from within. This is easily effected, as the experiments of Dalton and Graham show that a moist membrane is no hindrance to the penetration of a gas. In this way an absorption of foreign substances originates which is entirely independent of the peculiar nutrition of the cell. It may be a question as to whether other gases, as, for instance, carbonic acid, are not taken up into the cell in this manner. It is very certain that through this oxidation the substances are thus brought into a new relation with each other, and a new play of chemical activities is introduced.

* Organische Chemie, p. 85.

### III. *Of the Excretion of Substances from the Plant-Cell.*

§ 35. The endosmose whereby fluids are introduced into cells necessitates an exosmose, consequently a small quantity of the contents of the cell pass out. In this case there is no elective power of the cell to be assumed, but all that is dissolved in the cell, with the secreted matters, are exposed to a modification which, as in endosmose, is regulated by the relation of the substances in the inside to those on the outside of the cell.

In this place we must speak of the theory of excretion by the roots. But, first, we must regard this process as it takes place in the individual cell, for of such is the external part of the root composed. In this case we find that where endosmose takes place there also exosmose must exist; and the denial of excretion by the one process whilst absorption is admitted by the other, as is done by Meyen*, is highly unphilosophical. This, however, is a different question from that as to whether the plant has the power of rejecting those substances which are injurious to its life. We cannot conceive of an endosmose without an exosmose; but there is no sense in which we can say that the plant has the power of getting rid exclusively of that which is injurious to it, because the assumption of injurious and non-injurious substances is altogether gratuitous.

The substances which are thrown out from the cell during exosmose may become changed at the moment of their exit by contact with the substances passing inwards, so that in many cases it is not improbable that it is impossible to learn what is truly the product of exosmose. With this case we have one remarkable analogy. During the process of germination, starch, by virtue of the gluten (diastase), is converted into dextrin, and this again into sugar, and the sugar is ultimately converted into other substances, during which changes carbonic acid is fixed, and acetic acid is set free (according to Becquerel); at the same time acetic acid is never found free in germination. In fermentation the gluten changes the starch into gum and sugar, and separates this into carbonic acid and alcohol, which is easily (as, for instance, with soft platinum) converted, in contact with oxygen, into acetic acid. The analogy is so striking in this case, that we cannot avoid supplying by hypothesis the failing link, and supposing that alcohol also is formed during germination, and is immediately converted by union with oxygen into acetic acid, which is then separated.

Two points demand attention here, which modify the process of exosmose considerably. The one is the decided affinity between substances without the cell, and which are free to follow this attraction; and, secondly, the attraction which similar substances have for each other. In a fluid in which two salts are dissolved, we may produce a crystallisation of either one or the other, according as we throw into the solution a crystal of one or the other. In this way a cell appears to give out especially the matters which are found surrounding it in greatest quantity. At least, in this way we may explain the fact that the cells surrounding the gum-passages secrete the largest quantity of gum. These points will be reconsidered when we speak of the root.

* Physiologie, vol. ii. pp. 27. 524.

§ 36. When free gases are present in the cell in larger quantities than can be held in solution in the fluid, they naturally pass through the cell-wall, which presents no hindrance to their escape. When the fluid is saturated with gas, the nature of the gases in the neighbourhood of the cell determines whether, according to the law of equilibrium of gases, a partial interchange takes place or not. The gases which are combined in this way are principally oxygen, carbonic acid, and hydrogen.

The most universally present processes in the cells of plants are the decomposition of water, with the fixation of hydrogen, and the decomposition of the assimilated matters by the formation of carbonic acid.* Sometimes, as in the *Fungi*, the decomposition of water is attended with the liberation of hydrogen.† From hence it arises that, with the water of the plant-cell, the gases which are dissolved in it are also taken up. Thus we constantly find free gases which do not unite as in other chemical combinations, but which must also pass out free. This process occurs in its simplest form in the vegetating cells of the *Confervæ*, where carbonic acid gas is taken up, and oxygen gas is given out as the consequence.‡ In this case, the Daltonian law of the interchange of gases cannot be taken into consideration, because the quantities do not correspond with the law.

A fluid consisting of a solution of equal parts of gum and sugar, when saturated, would contain about 70 per cent. of carbonic acid. When this becomes fixed, about sixty-three volumes must be set free in the form of oxygen gas, so that the carbonic acid is diminished nine-tenths of its bulk by the loss of oxygen. De Saussure's experiments prove that this is about the relation which the carbonic acid and oxygen bear to each other. There are, however, many circumstances which may modify this process to some extent, and especially the interchange of gases according to the law of Dalton. This process is sometimes called, with great impropriety, respiration, and is supposed to resemble the same process in animals. The phenomena become much more complicated when, in addition to the simple process of decomposition which goes on in the cell, some of the contained substances, as, for instance, resin and the like, absorb gases, as oxygen, from without, and unite with them.

## IV. *Disposition of the assimilated Matters.*

§ 37. The plant-membrane grows through the assimilated matters in such a way that it is extended equally on every side, so that a still larger space is surrounded, and its walls become thickened.

The cause of growth in this case is apparently from the attraction of similar substances for each other, as seen in the increase in size of crystals when placed in solutions of the same salt. The absorbed matters do not, however, arrange themselves in regular layers upon the surface of the membrane, but permeate all parts of the absorbent membrane in a semi-fluid state; but still the increase of surface is greater than of thickness. In this way a cell continues to grow without its walls becoming thicker. We have no grounds to suppose that isolated cells grow through apposi-

* See Germination.

† Humboldt, Floræ Fribergensis Specimen, p. 179.

‡ First observed by Priestley, in the year 1773. See Priestley, Observations and Experiments on various Kinds of Air.

tion, but much more evidence to prove that this process takes place by a true intus-susception. Schwann has made some highly ingenious researches on this subject.*

§ 38. At a definite period, the cell-membrane ceases for the most part, or entirely, to grow; and the assimilated matters, which are so formed that they pass readily into a solid form, distribute themselves in a special layer upon the inner surface of the membrane, in the various forms we have already spoken of (§ 16.). This process goes on as long as new matters are formed.

In the formation of crystals, we find that the constantly increasing layers are deposited only of a definite thickness, and when this thickness is reached the formation of a new layer begins. We find the same taking place in the plant-cell; only with this difference, that in the cell the solution is in the interior, and the newer layers are deposited from within. Of the cause which gives to these deposits a spiral form we know little or nothing; only this much we can say, that neither in round nor longitudinal *isolated* cells are either deposit-layers or a spiral arrangement exhibited. The first indication of a spiral direction of parts is seen in the species of *Spirogyra;* but here the spirally deposited matter is not the formative matter of the cell, but chlorophyll.

It often happens that the primary cell-membrane continues to grow after the second layer is deposited, which results in a division of the last layer if it has not grown equally with the first. When a new layer consists of another modification of the assimilated matter, or the first layer becomes dry and firm before the second is deposited, a greater or less evident separation between them is visible.

§ 39. The matters contained in the cell serve not only for the completion of the cell itself, or for the formation of new cells (§ 13.), but also constitute, in various conditions of aggregation, and under multifarious forms, the contents of the cells. In the organic substances the fluid portion is very gradually transformed into a relatively speaking firm, but not completely solid, matter. The unazotised compounds, gum, dextrin, jelly, amyloid, starch, &c., are rendered firm by the gradual abstraction of the solvent (water), and, in a similar way, from the azotised compounds, is formed the mucus. In consequence of this process of change, many of these substances appear in remarkably defined forms, requiring especial notice. Besides crystals of inorganic salts, we observe, in the cells, starch-, inulin-, and mucus-granules, larger globules of gum, resin, and oil. But the most remarkable of these forms is one of a peculiar character, assumed by the mucus in certain cells of the antheridia in the *Characeæ*, Mosses, Lichens, and Ferns, in which it presents the aspect of a spiral filament, with from one to two turns and a half.

The contents of the individual cells exhibit an endless variety, from a mixture of many very different fluid and solid constituents to a single nearly uniform material, either liquid or solid, occupying the whole cell.

* Mikroskopische Untersuchungen, p. 229.

Individual cells are frequently entirely filled with essential oil or with resin, or with a substance not yet chemically determined, of a red or brownish colour, which is found in the cells of many *Algæ* (the hologonimic cells of Kützing). In the green cells in a state of active vegetation, the following appearances are usually observed: the internal surface is invested with a continuous and very delicate layer of semifluid mucus ("amylid-cell" of Kützing, "primordial utricle" of Mohl), to which the more solid mucus and starch granules adhere; these granules are usually covered by chlorophyll in a semifluid state, or that substance is attached to the mucous layer, occasionally, as in the species of *Spirogyræ*, in spiral bands jagged at the edges.* The chlorophyll may be merely deposited *upon* the starch, or it may be, perhaps, that starch is formed *into* chlorophyll, but never *from* it. Chemistry is wholly opposed to the latter being the case (§ 12. 1.). The rest of the space in the cell is usually filled with a thin, tolerably clear fluid — a mixture of dextrin, sugar, and albumen in solution, in the most varying proportions; and not unfrequently also containing more minute, semifluid, mucus-granules, inulin, extremely minute oil-globules, and chlorophyll, distributed in various ways: inorganic crystals, on the other hand, are rarely met with in cells in a full state of vitality (as is sometimes the case in *Spirogyra*). Of these matters, however, one or the other is occasionally wanting, or exists in greater or less proportion. Crystals, especially when in great numbers, usually occur only in an aqueous fluid containing few organic compounds, as, for instance, dextrin: oil and resin are frequently found alone. As to the forms exhibited by these substances, all that is necessary has been already said (§ 7. 9, 10.): I will here merely notice, in addition, two very remarkable conditions.

*a.* Upon examining the fibres of the root of *Neottia Nidus avis* (in flower), three layers of cells will usually be observed immediately beneath the epidermis; the first consisting of cells about three times as long as the epidermis cells, and of the same breadth; the second and third, of cells of the same length as the former, but as broad as long. Immediately on the inside of these succeed cells of the same breadth, but three or four times longer, containing starch. Each cell of the outermost of these three layers contains an elongated irregular mass of a semi-solid yellowish substance (coagulated mucus?), which occupies nearly the whole of the cell. Each cell of the internal layer is filled in the same way, but in them the contents are intermixed with distinct fibres. The cells of the intermediate layer, lastly, contain a globular mass of a material of a browner colour which almost fills them; this globular mass is not composed of an amorphous substance, but, on the contrary, is constituted almost entirely of interlaced fibres, very similar to those which occur in the internal layer of cells. These fibres, which at first sight might be taken for spiral fibres, are seen, on stricter examination, to be, in the first place, all confusedly entangled, and, secondly, to be not solid but to constitute tubes with unyielding walls and of moderately wide calibre. They frequently present irregular dilatations and short lateral cœcal branches, and they not unfrequently subdivide into longitudinal branches. They also exhibit dissepiments at regular distances, especially towards their extremities, which are rather dilated; these dissepiments

* Kützing's notion that the amylid-cell is contracted into these spiral bands (Phycologia generalis, p. 49.) is to be attributed to the want of precise observation. The soft mucus investment co-exists in a perfect state together with the spiral bands.

are composed of a bright yellow substance (mucus?), so that the fibres do not altogether appear unlike some *Confervæ*. With respect to the real character of these peculiar formations I have nothing at all to observe. The system of vessels discovered by Gottsche, in *Preissia commutata*, may be adduced as the only thing at all analogous to them, but just as isolated and mysterious. In this case the individual cells are traversed by similar tubes, which appear to perforate the cell-wall itself. In either case, an elucidation of the mystery can be expected only from tracing the course of development.

*b.* In the antheridia of the *Characeæ*, Mosses, and Lichens, as well as of the Ferns, the layer of mucus is apparently transformed, in the tender cell, into a spiral filament; the history of which has, as yet, been by no means rendered clear. Its relation to the soft mucous layer especially, still requires more particular investigation; and it might also probably be a question for determination, whether the cells in which these spiral filaments are developed are in reality perfect cells or only the nuclei of cells, that is to say, hollow cytoblasts. The best recent researches on the subject are those of Nägeli.*

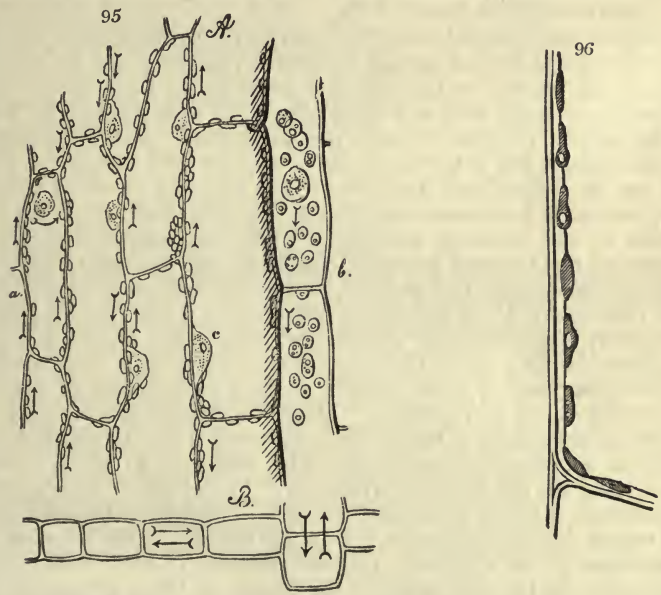
## V. *Motion of the Cell Contents.*

§ 40. The fluid contents of vegetable cells exhibit two kinds of motion, as to the causes of which we are still wholly in the dark. In most plants in the families of the *Characeæ*, *Najadacæ*, and *Hydrocharidaceæ*, there is observable in each cell a single current ascending on the one side and descending on the other, the fluid constituting which, differs in colour, consistence (mucosity), and insolubility in aqueous fluids, from the remainder of the transparent cell-juice. The current is rendered more evident, in some cases, from its carrying along with it the spherical bodies contained in the fluid (starch, chlorophyll, mucus, &c.); but for the most part it is sufficiently evident of itself.

The motion is best seen in the species of *Nitella*, in the hairs on the roots of *Hydrocharis morsus ranæ*, and in *Vallisneria spiralis*. Each, however, has its peculiarities. In *Nitella* the moving stream is very considerable, so that only a narrow streak remains at comparative rest between the ascending and descending currents. The stream is strong and rapid, and carries along with it starch-granules of considerable size. Its course is not exactly parallel to the axis of the cell, but forms a small angle with it. In two contiguous cells the currents flowing on the partition between them run in opposite directions, consequently throughout the whole plant the ascending streams are on one side, and, in fact, owing to their oblique direction, form a spiral; this is the case also with the descending streams. When very young, the cells are perfectly transparent, a condition which they subsequently lose, in consequence of numerous granules, covered with chlorophyll, arranging themselves in slender parallel rows upon the walls exactly in the course of the streams, and leaving on each side only the narrow interspace between the streams

* Schleiden und Nägeli, Zeitschrift für wissenschaftliche Botanik, Bd. I. Heft. I. S. 168. et seq. This paper is translated by the Ray Society in "Reports and Papers on Botany," 1845.

uncovered. If the cell be carefully tied across, the current is in a short time re-established in each subdivision. If the cell be cut through, the circulating fluid escapes only on one side from the stream which is directed towards the opening, the remainder of the fluid completing its entire circuit through the cell before it also comes to escape. Any influence detrimental to the life of the plant also affects the motion of the sap, and whatever favours the former also promotes the latter. The same thing, in all respects, takes place in *Chara*, only that in this plant the observation is not so readily made. In no plant in which the circulation is in any way exhibited are the currents found to be so associated as to constitute an ascending and a descending spiral. In *Hydrocharis*, owing to the perfect transparency of the naturally isolated cells of the hairs of the roots, the observation is exceedingly easy. In *Vallisneria* (figs. 95, 96.), although the leaf must first be cut parallel to the surface, in order to render it sufficiently transparent for convenient observation, this proceeding is not detrimental to the motion, which, after a few minutes, is again exhibited in its pristine activity. In this plant the circulating mucous fluid is very scanty, and constitutes merely a very thin covering on two opposite walls; but it has sufficient power to carry on the usually flattened lenticular granules covered with chlorophyll, and which are of tolerable size.




[95] *A*, Section parallel to the surface from the leaf of *Vallisneria spiralis*. In the cells from *a* to *e* is seen the current of sap, the direction of which, as observed in each cell, is indicated by the arrow. In the cells marked *b*, which form the lateral boundaries of the air-passage opened by the section, the anterior half only of the current is seen in its whole width. The very gelatinous cytoblast circulates with the stream. *B* exemplifies the same section on a ground plan.

[96] A portion from the section shown in fig. 95. more highly magnified. The thickness of the stream exceeds that of the double cell-wall: the elongated, roughened corpuscles are the lenticular granules of chlorophyll carried along with the current; at the same time their varying figure and various positions in the circulating fluid are exhibited.

In *Najas major* and *Caulinia fragilis*, in the fruit-stalk of the *Jungermanniacæ* (according to Meyen), the motions are precisely of the same kind. The observation is of extreme difficulty in *Stratiotes aloides;* and after frequently repeated examination of every species of *Potamogeton*, I have only twice succeeded in actually seeing the motion: I have, unfortunately, forgotten to note the species.

After the most careful research with the best instruments, I have been unable to perceive a trace of the presence of vibratile cilia as a cause of the motion, and it is very improbable that such should exist. Whenever these cilia are found in animals and plants, they always appear as processes on the exterior, never in the interior, of cells.

This kind of circulation, taken as a whole, seems to be, for the most part, a phenomenon wholly peculiar to the vegetable-cell, and to be connected with its perfect individuality. All the plants above mentioned, in which the circulation is observed with certainty, are aquatic, or else very fond of water, belonging to families very low in the scale of organisation, in which the cells exhibit a great degree of independence, so that separated portions of the plant (for instance, of the leaves of *Vallisneria*) often retain their vitality for months. The supposed circulation of the same kind in higher terrestrial plants I must for the present leave undetermined, as I have never been successful in making even a single observation with regard to it.

*Historical and Critical.* — In the year 1772, Bonaventura Corti discovered the circulation of the sap in certain *Characeæ* and in *Caulinia fragilis* ("mia pianta," as he constantly terms it), and also extended his observations to many land and water plants, the determination of which is, at the present time, for the most part impossible. Fontana confirmed these discoveries, and at the same time cleared up some errors into which Corti had at first fallen. Both these inquirers had observed so accurately, and made such numerous experiments, that their successors were not able to add anything essential. Their discoveries, however, in the times of the Linnæan school of compilers, were so totally forgotten, that C. L. Treviranus, first in 1807, rediscovered the motion of the sap in the *Charæ*, and Amici in 1819 in *Caulinia;* to which instances Meyen subsequently added the other plants enumerated, after Horkel had again fallen upon the writings of Corti, and drawn attention to their contents.

Corti's observations, above alluded to, upon land plants, as has been said, do not admit of repetition. Meyen* formerly said a good deal about these observations, that he had confirmed them all, without at the same time entering into particulars, with reference to which I would remark, that at the time he wrote his "Phytotomie" he was unacquainted with the kind of motion described in the following section, or, at all events, did not distinguish it from the other. In his last work† he passes it over in, as it appears, prudent silence. In his "Prize Essay" he states that he has also observed the motion in *Pistia Stratiotes.* He and others have repeatedly confounded the circulation here described with the following.

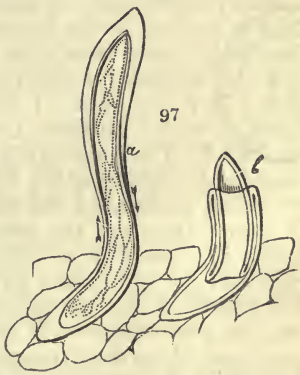
Corti's notion, which was opposed even by Fontana, that the ascending and descending streams are separated by a septum in the cell, has been repeatedly broached since his time, but it is easily shown to be false.

* Meyen, Phytotomie, S. 182. Ueber die neuesten Fortschritte der Anatomie und Physiologie. Harlemer Preisschrift, 1836, p. 165, and elsewhere.

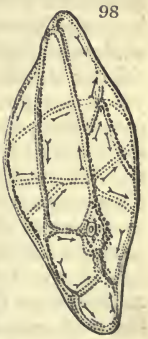
† Physiologie, vol. ii. p. 206, et seq.

The fanciful opinion propounded by Amici, Dutrochet, and others, of the motion being caused by a galvanic influence, in which the rows of chlorophyll globules in the *Charæ* represent the connecting chain, is an unscientific sporting with lame analogies. It is at once refuted by the fact, that in the germinating *Chara* the circulation is evident previous to the existence of the globules and their serial arrangement.

§ 41. In almost all cells which, according to their position or degree of completion, enjoy a high degree of independence, a peculiar system of minute currents, with numerous anastomosing branches, is exhibited. The fluid of which these currents are constituted is of a mucous nature, mixed with minute opaque granules; and the streams proceed from, and return to, the cytoblast, which is invariably present at the same time: they cover the internal surface of the cell-wall (fig. 97.), or traverse the cavity of the cell from one wall to the other, without mingling with the rest of the cell-fluid, which is for the most part as clear as water.




Up to the present time, I have found this peculiar form of circulation in numerous cryptogamous plants, for instance, in *Achlya prolifera*, *Spirogyra*, and other *Hyphomycetes* and *Confervæ;* in almost *all* the forms of hair in the *Phanerogamia* (Plate I., fig. 13.) that I have as yet examined, for instance, in *Solanum tuberosum;* in many spores, such as of *Equisetum arvense*, and pollen granules, for instance, of *Œnothera grandiflora* in the immature state; in almost all immature endosperm-cells, as in *Nuphar luteum*, and especially in such as are subsequently. reabsorbed as in *Ceratophyllum demersum*, in almost all stigma-papillæ, as in *Tulipa Gesneriana*, in the loose cells of juicy fruits in the young state, as in *Prunus domestica;* in the pulp which is constituted by the placental cords (Plate I., fig. 7.), as in *Mammillaria;* less frequently in the loose juicy parenchyma of many plants in the young state, as in *Tradescantia rosea*. I believe it exists, however, in all vegetable-cells as long as the cytoblast retains its vital activity. Upon the whole, I have, up to the present time, collected several hundred examples from the most various families.




As instances admitting of easy verification, I would mention the fruit of *Symphoricarpos racemosa* (snowberry) (fig. 98.), which may be procured anywhere, or of a *Mammillaria*. Each cell in these instances is entirely

[97] Longitudinal section through the style of a *Campanula*, with two hairs: *a*, a hair exhibiting a circulation; its point is enclosed in a layer of mucus: *b* has lost its contents, and is in consequence contracted.

[98] A single cell from the fruit of the Snowberry: the arrows give the direction of the currents.

isolated, and filled with a colourless clear fluid. At one part of the wall is affixed a sharply defined, faintly granular cytoblast, presenting a well-marked nucleolar corpuscle. The cytoblast is always surrounded by a narrow areola of a yellowish mucous fluid, thickly crowded with minute opaque granules, and from it proceed currents of various width and depth. At the margin, and consequently where the cell is viewed from the side, these currents are often seen to advance with distinct minute undulations: the direction of some of the currents is from the cytoblast, of others towards it. In their course they exhibit numerous branches, and anastomose with each other: in these plants only rarely, but in others more frequently, separate currents traverse the cell, in order to unite with other currents on the opposite side. Many of the streams are so minute, that under the highest magnifying power they exhibit the appearance of a line without any breadth, merely rendered to a slight extent irregular by the individual granules. Occasionally a current is suddenly interrupted, the leading portion continuing its course; a minute drop of the fluid is then formed at the extremity of the remaining portion, from which, after some time, the current is continued in the former or in a new direction, or else two or more currents proceed in a new direction. In this respect, all other cells present merely unessential differences, of which, however, the most interesting is exhibited in *Ceratophyllum.** There are certain facts that must be borne in mind, in future attempts at explaining the nature of the motion described in the two preceding paragraphs, and which may probably lead to the explanation of them: these are the endosmosis and exosmosis, which must necessarily, in some way or other, give existence to a motion of the cell contents; the continuous formative agency of the cytoblast, the peculiar nature of the circulating fluid, its immiscibility with the watery sap, its great adhesion to the cell-walls, as well as its great intrinsic cohesion. At present it must be confessed, however, that we are not in a condition to construct any useful theory out of these elements.

As far as it can be determined with certainty, the circulating fluid appears invariably to be mucus (albumen?). When cells, in which is exhibited the circulation described in this and the preceding section, are submitted to the action of alcohol or nitric acid, the mucus contracts on its coagulation, and may be observed to invest the whole surface of the walls with a thin layer, and the currents will be seen to constitute merely thicker streaks of mucus. The same thing takes place in every cell as yet immature. Both in the latter, and in those cells which exhibit a circulation, the cell-contents frequently coagulate of themselves, in consequence of chemical processes in the cell, and then retract spontaneously from the walls. In cells undergoing lignification the mucus gradually disappears. In all young cells the mucous investment may be demonstrated also by the use of iodine. Might not its existence be said always to indicate motion? What phytotomist can have overlooked the innumerable instances of cells in which mucous filaments radiate from the cytoblast? Whenever I have examined these cells in the earlier condition, I have *never* failed, with due perseverance, to observe the circulation in these mucous filaments, or rather streams. The mucous layer in question is frequently so little granular, that its motion

* See my "Beiträge zur Kenntniss der Ceratophylleen in the Linnæa," vol. ii. (1837), p. 527, et seq. Botanische Beiträge, vol. i p. 213, et seq.

is scarcely at all observable. May not this motion be regarded as a universal phenomenon, and as most intimately connected with the assimilation of the azotized matters?

*Historical and Critical.* — This form of sap-motion was discovered by Robert Brown in 1831, in the hairs of the filaments of *Tradescantia virginica.** Slack, Meyen, and myself, have contributed the principal additions to the number of instances. Meyen thinks that, besides these sap-currents, air is contained in the hair-cells in *T. virginica;* but this is altogether erroneous. His attributing an assertion to the same effect to Robert Brown†, arises simply from a mistranslation of the English: Robert Brown refers merely to the air which is adherent to the hairs. Slack‡ supposed that the hair-cells of *T. virginica* contain a second utricle, and that the currents flow between its wall and that of the cell. Accurate observation easily shows this view to be a mere fiction. The most superficial observation only, or the most defective microscope, could have led Schultz§ to misplace these currents on the outside of the cell, in a special system of vessels (his "vasa laticis contracta"). A single attentive observation is sufficient to refutet his notion, and to demonstrate the phenomena as I have described them, as well as the impossibility of the existence of such a system of vessels. Meyen ascribes the motion not to the fluid, but to a self-motive power inherent in the granules that are carried round with it; an idea which, in some cases, has led to his overlooking the fluid. But views of this kind I regard as being without any foundation whatever.

I make no reference to the dispute as to the *existence* of either this or the previously described motion, any question upon the subject being altogether out of date. Whoever, at the present day, entertains a doubt about it, is quite unfit to make any physiological observation.

§ 42. The spiral filaments in the antheridia of the *Characeæ,* Mosses, *Hepaticæ,* and Ferns, mentioned at the end of § 39., exhibit, at least when in contact with water, a peculiar motion, consisting principally in a rotation around the axis of the spiral, and which motion in the free filaments is shortly changed (according to the law of the Archimedean screw) into a progressive movement; but the motion is modified in divers ways, according to the varying width and diameter of the spirals.

The motion referred to in the section is as yet, together with the existence of vibratile cilia, one of the most remarkable and mysterious phenomena in the vegetable world. Phenomena of this kind afford but too ready a ground for the unbridled fancy to fill up the defective gaps in our knowledge, with what are termed clever notions; the divine maxim of St. Paul, "that we know in part," being disregarded. Many fabulous statements consequently have, in former times, been made on this subject. Too much caution, therefore, cannot be employed when *apparent* analogies are indicated, lest they should be received as views having a scientific foundation, and used in the erection of a

* On the Sexual Organs, &c. in the Orchideæ and Asclepiadeæ (1831), p. 172.
† Physiologie, Bd. II. S. 244, et seq.
‡ Transactions of the Society of Arts, &c., vol. xix. (1833).
§ Flora, 1834, p. 120., and his Paris prize essay upon "Cyclosis."

farther superstructure. I myself always prefer as much as possible to refrain from this play of an active fancy, rather acknowledging my ignorance, and endeavouring to show that it arises inevitably from the nature of the thing itself. As in every thing else, however, theoretical views of one sort or another have abounded respecting the phenomena in question.

In the first place, we are not even acquainted with the morphological significance of the organs in which the delicate cells, with spiral filaments, are developed. We know just as little about the development of the cells; are just as, or perhaps more, ignorant regarding the formation of the spiral filaments; and with respect to their chemical nature, we are able to arrive at only a very imperfect probability. As to the mechanism of the motion, we know just as little as we do of that of the moving cilia: of the cause of motion, of the motive power, just as much as that of the contraction of the primitive muscular fibre, of the motion of animal spermatic filaments, and of the vibratile cilia on animal and vegetable cells;—that is to say, absolutely nothing. A comparison of this motion with that of the heavenly bodies, is, however, wholly inadmissible, because the commencement of the motion in the organisms in question has relation to time, but not so that of the heavenly bodies; on which account, with respect to the latter, the question after the first impulse (tangential force) does not concern us at all, but it *does* very materially with respect to the organic structures. All these motions fall into the same category, in every respect, with those which will be described in the following section. Ignorance and stupidity term them "primitive phenomena." The discreet and profound investigator of nature recognises their temporary limitation in this respect, as well as their destined application to purposes of further activity.

§ 43. When a multitude of very minute corpuscles of either an organic or inorganic nature, for instance, minute starch-granules, small crystals, &c., are contained in a cell in a fluid of sufficient tenuity, they usually exhibit a quivering motion (termed "molecular motion"), the cause of which is still unknown to us; but in any case it has no necessary or exclusive connexion with the life of the cell.

Some observations relative to this subject had been made at an earlier period, but had been either disregarded or at least not followed up, and it was not till 1827 that R. Brown* first took up this phenomenon in a connected point of view, and at the same time completed the inquiry so fully, that scarcely any thing remained to be added; and it required the subjection of a Meyen to preconceived notions to speak of it as a vital phenomenon.

All bodies sufficiently minute, organic or inorganic, and suspended in a fluid not too thick, present a peculiar oscillatory motion, unattended with any perceptible change of place. Instances of this phenomenon are to be found in almost all plants, in the mucus- and starch-granules, crystals, &c., whether inclosed in a cell or free; but only when the fluid can retain them in suspension, so that they cannot sink to the bottom. The milky juice, and that contained in the pollen grains, are fluids eminently of this nature, and in these, consequently, the motion in question is most

* Vermischte Schriften herausg. von Nees v. Esenbeck, vol. iv. p. 143.

frequently and most readily observed. As it happened accidentally that these motions were first observed in the latter organs, as being more frequently and more particularly examined than the common cells, fancy was at once busied in erecting therefrom all sorts of wonderful systems. It is to these motions that those amongst us who are gifted with speculative heads are indebted for the vegetable *Spermatozoa.* But it is to be hoped that we shall soon be delivered from them, as such true and sober observers as Fritsche* and Nägeli† for plants, and Kölliker‡ for animals, have declared war on good grounds against the animality of the *Spermatozoa.* That the supposed change of form of the minute, elongated, crescentic starch-granules in the *Onagraaceæ* depends upon optical illusion, is easily ascertained by the attentive and unprejudiced observer. There can be no question as to its not being a vital phenomenon, because the motions continue even in the alcoholic tincture of iodine (an absolute poison for all vegetable and animal life), of which any one may readily convince himself, and which Fritsche § has, with his well-known accuracy, shown to be the case in a great number of plants. No person but one blinded by preconceived notions, and looking every where for prodigies, and especially not under the cautious guidance and support of a sound philosophy of nature, can find anything extraordinary in the perfectly natural occurrence of this universal physical phenomenon in the contents of the pollen-cell, or endeavour, with empty fancies, to supply the gap which he imagines nature to have left.

Respecting the ultimate cause of this phenomenon we know nothing at all; electrical tensions and the balancing of electrical forces, consequent upon chemical processes, have been provisionally proposed as an explanation. It is better to wait and direct our activity to something else, than to waste our own and others' time with premature views and untenable fictions.

## VI. *Motions of the Vegetable-Cells.*

§ 44. In the spore-cells of certain of the lower aquatic plants, there is exhibited, for some time after their quitting the mother-cell, occasionally also some time before their doing so, a locomotion resembling the molecular movement; but with the difference, that in this case the motions are more considerable, and effected by means of vibratile cilia.

Perhaps in no case has the want of sound philosophical principles led to greater phantasies than in the above phenomenon. The subject has become still more involved by the statement in former times of a multitude of supposed facts, the immediate offspring of imperfect observation, and which had no actual existence. Meyen, to whom we are indebted for a very industrious compilation of all that has been said on the subject, (Physiologie, vol. iii.) says that he found himself compelled to make a

* Ueber den Pollen. St. Petersburg, 1837. From the Mém. de l'Acad. Imp. des Sc. de St. Pétersburg, printed separately, p. 24, et seq.

† Zur Entwicklungsgeschichte des Pollens bei den Phanerogamen. Zurich, 1842.

‡ Beiträge zur Kenntniss der Geschlechtsverhältnisse und der Saamenflussigkeit wirbelloser Thiere, u. s. w. Berlin, 1841, p. 49.

§ L. c.

critical selection of the facts, but afterwards goes to work as uncritically as possible. Two circumstances conduce to render the earlier observations of Ingenhousz, Agardh, Wrangel, Wilke, Girod-Chantrans, and others, entirely useless, or, at all events, very suspicious; in the first place, because the above-named observers were not sufficiently assured of the identity of the motionless and moving corpuscles, and secondly because, owing to the then state of science, and the nature of their instruments, they were not at all in a condition to distinguish between true *Infusoria* and the minute spores of the *Confervæ*, &c. To which, also, may be added that, as regards the *Confervæ*, many things have been looked upon as spores which were merely cell-contents, as starch, chlorophyll-granules, &c., and which consequently, very naturally, occasionally exhibited the molecular motion.

As a proof of the good grounds I have for this scepticism, I would merely remark, that an observer like Kützing, who has devoted thirteen years, with the most unwearied industry, to the observation of the *Algæ*, ventures to state in his whole work but three instances in which he himself had an opportunity of observing the phenomenon in question.

As facts of a more certain and useful nature, only a few observations remain, in which it was noticed that the spore-cells were liberated and exhibited spontaneous motion, but afterwards became motionless and germinated. The latter circumstance especially must necessarily be inquired into in referring to the older observations, because we also know as a fact that true *Infusoria* are actually met with in the interior of the cells of *Confervæ*. Acting in an earnest spirit of criticism, which alone will suffice to secure us from being misled by the dreams of fancy, I can admit but very few of the facts adduced by Meyen in his "Physiologie" and Annual Reports, all of which have reference to spore-cells, partly of the *Confervæ* and partly in the filamentous *Fungi*. To these, also, are to be added some later observations by Unger *, Kützing †, and Thuret ‡. I have succeeded in observing a phenomenon of the kind in question in two plants only, viz., in *Achlya prolifera* and *Vaucheria clavata* DeC. This observation is quite sufficient, however, to place the fact itself beyond doubt. *Achlya prolifera* presents two kinds of spores: larger ones, which are formed in smaller number in spherical sporangia; and smaller ones, which are developed in greater numbers in the unchanged filiform terminal joints, from which, when the spores are mature, a minute operculum is detached. Shortly before this, the spores assume a vibrating motion, which is accompanied with change of place, often considerable. This motion lasts for some time after the spores have escaped, and finally ceases, whereupon the spores frequently, even after a few hours, begin to germinate. When a terminal joint of this kind is emptied, a new similar joint usually grows within it, arising from the next septum, and frequently not wholly filling the remaining former one. In this new joint, also, spores are again formed, which have then, in making their escape, to pass two openings, and occasionally move about for a long time between the two cell-walls before they reach the second opening. But it also happens, that they never arrive at this second opening at all, and germinate, or at least begin to germinate, within the older utricle.

* Unger, Die Pflanze im Momente der Thierwerdung.
† Kützing, Phycologia generalis.
‡ Thuret, Les Organes Locomoteurs.

In *Achlya prolifera*, no observation has yet been published serving to throw light upon the mechanism of this motion; my own observations date at a period in which I first began the pursuit of Botany. In *Vaucheria clavata* I have only *once* observed a liberated and spontaneously moving spore, and immediately noticed currents on each side of it, rendered manifest by the rapid transit of minute corpuscles. I thereupon concluded that these currents were produced by cilia, but in trying to fix the spore and observe it more closely it was unfortunately destroyed. Unger, and, after him, Thuret, have communicated more particular observations on this subject, and shown that the whole exterior of the cell is covered with vibratile cilia. Thuret has also observed motion and vibratile cilia as the cause of it in *Conferva rivularis* and *C. glomerata*, in two species of *Chætophora*, and two of *Prolifera*. (?) Kützing simply noticed the motion in *Achlya prolifera*, *Tetraspora gelatinosa*, and *Ulothrix zonata*, without making any observation on its cause. Excepting in those of *Achlya prolifera*, *Vaucheria clavata*, and *Tetraspora gelatinosa*, Kützing and Thuret found in the self-moving spores a reddish spot, like that in the green monads, and termed by Ehrenberg "eye-points." Kützing observed this spot in the spores, not only whilst yet in the sporangium, but also even in the first or second cell of the spore when becoming developed into a *Conferva*. All these spores, except those of *Achlya prolifera*, are green; whilst Kützing states it as a law, that in all the lower *Algæ* (his *Isocarpeæ*) the true and mature spores are brown. More precise and comprehensive observations on this phenomenon are still indispensable before any conclusive result can be drawn from them. Are there not probably spores whose completion is not yet effected, in which the formation of the cell-membrane from the tender mucus-layer has not been as yet perfected, which lose their cilia (mucus?) and become capable of development as soon as the formation of the cell-membrane is quite completed?

The lower *Confervæ*, filamentous *Fungi*, &c., have at all times afforded the most fertile field for the mystical dreams of fancy, because in no part of Botany are researches so difficult to make, and so much out of our power to control. Here, more than any where else, it is necessary, in order to escape all unscientific, fanciful delusions, to be guided by the maxims of a sound philosophy. Particularly is it necessary in this case, if we do not wish to deprive scientific research of all certainty, at once to dismiss from consideration every observation that has not been made upon indubitable *plants*. I have consequently, in considering this question, as elsewhere, left entirely out of the field the *Diatomaceæ*, *Bacillariæ*, &c.; in short, all those forms the animal nature of which has been asserted by Ehrenberg, upon grounds at all events worthy of consideration. Whoever is interested in this subject, will find in the masterly works of Ehrenberg, especially in his great one on the *Infusoria*, as well as in the diligent labours of Kützing, a great mass of historical matter, collected with the most extraordinary industry, together with abundance of remarkable original observations. As a basis, however, for the foundation of *botanical* laws, these materials should not be employed.

Only a science crazy with fantastical mysticism, and far removed from a clear, self-intelligible Natural Philosophy, could entertain the dreamy notion that creatures may be at one time animals and at another plants. Were this possible, it would necessarily much more readily happen that a being should be now a fish and now a bird; or at one time a conferva, at another a rose; and then what would all our natural science be but

folly! This perplexity of ideas, correctly and most happily designated by Valentin (Repert. Bd. 8. S. 4.) as Anachronism, has latterly been carried to a great length by Unger (Die Pflanze im Momente der Thierwerdung) and Kützing (Phycologia generalis). It can only be regretted that such able inquirers should be so entirely without any philosophical insight.

Lastly, when, in the mention of facts of the nature in question, we meet with the expressions "the cells move spontaneously here and there," &c., it shows us how obscure and perplexed so many men even of the greatest scientific acquirements may be. We discover spontaneity only in our minds by self-observation. In animals, analogy leads us to conclude its existence, from our observing actions having a definite object; and yet in this case the subject is attended with a sort of mystery, for there is nothing by which we can know that the object was really aimed at by the animal itself. No reasonable man, however, believes that the planets designedly pursue exactly this or that course, and with exactly the proper degree of rapidity or slowness, to prevent the possibility of mishap; and yet an object is attained by their motion — the maintenance of the solar system. But, with reference to motions by which in no case can any intelligible object be attained, to speak of "will" is a mere playing upon words.

## VII. *Reproduction of the Cell.*

§ 45. When a large quantity of soluble assimilated matter, together with the needful quantity of mucus, have been formed in a cell, the processes described § 23. necessarily recommence. One or several new cells (filial cells, *blastidia*) are formed within the cell (mother-cell, *matrix*), which is destroyed when the new cells have attained a sufficient expansion. Since it is a matter of course that a figure should depend upon the material from which it is constructed, and the conditions of its formation, and as both these are derived from the mother-cell, it necessarily follows that the filial cells are repetitions of, or resemble, the mother-cell.

If anywhere, it may certainly be here asserted that it is of essential importance in the treatment of a science to set each individual point in its appropriate place and in its proper light, to allow of the *whole* being correctly understood. As the scientific problem has never been put plainly and rigorously, nor the questions requiring answer deduced from it, the point referred to in the section has remained even up to the most recent period wholly untouched, and has in fact but just received some cursory notices; and yet in the whole vegetable kingdom there is nothing of more importance. With few exceptions, every plant consists of numerous cells; the beginning, however, of every plant is in a single cell, in the *Cryptogamia* the spore, in the *Phanerogamia* the embryonic cell. The question respecting the multiplication of the cells consequently includes the origin and the life of the whole plant, which remains altogether obscure to us previous to the elucidation of this relation. The mode in which one cell forms many, and how these, dependent on the

* See C. v. Siebold de Finibus inter Regnum Animale et Vegetabile constituendis. Erlangen, 1844.

influence of the former, assume their proper figure and arrangement, is exactly the point upon which the whole knowledge of plants turns; and whosoever does not propose this question to himself, or does not reply to it, can never connect a clear scientific idea with plants and their life. From the total neglect of this point it is no wonder that most of the notions in Botany are enveloped in a dark and formless mysticism.

The Protococcus-cell here again suggests the natural standard by which to judge of the most simple conditions. In it we may observe that two new cells are formed within the cell, which lie for a time loose in the mother-cell, and at last destroy it, and then become new, free organisms. The same thing takes place, according to Nägeli, in almost all the *Algæ:* a similar process is exhibited in the double spores of the Lichens. In the *Pezizæ* we may notice eight new cells originate in a cell. In the Ferns and *Equiseta* the spore-cells are formed in the mother-cell. In the *Phanerogamia* it is easy to observe the formation of cell within cell: in the embryo-sac (a large cell), in the embryonic-cell, in which the production of new cells within the first-formed ones may also be traced. In the pollen of most plants there is no doubt that free cells are formed in other cells; in the apex of the bud, and in the cambium, it not unfrequently happens that new-formed cells are seen in the mother-cell: almost all forms of hair entirely corroborate this view of the process. Examples of this sort are exhibited in nearly every group of plants, and almost in every part; and consequently I believe that the proposition based upon induction may be thus provisionally defined:—"*The process of the reproduction of cells by the formation of new cells in their interior is a general law in the vegetable kingdom, and is the foundation of the production of cell-tissue.*" Respecting the way in which new cells are produced, all that is necessary has been previously stated (§ 13.).

The figure of the incipient crystal depends upon the material of which it is formed, and the physical conditions under which it originates. This might, perhaps, be thus expressed in general terms: the figure depends upon the nature of the material and the nature of the formative processes. To apply it to the cell, as the matter and form of the originating formative process are derived from the mother-cell, the latter must exert an essential influence upon the filial-cell. The formation of the latter, however, is not completed in the mother-cell, but is continued after its liberation therefrom, and consequently the figure of the filial-cell is modified in many ways by after influences and relations. This explains both the constancy of the specific figure, and the multiplicity of the individual varieties. Here, consequently, we require nothing but the complete analysis of the process of cell-formation in its separate elements, and of the information to be derived from crystallisation (as, from a definite material and determinate physical condition, a determinate figure must inevitably arise), in order to subject to a scientific solution, and under the simplest form, the great mystery of organic generation, upon which the constancy of species, and together with it the normal conditions of the whole of organic life upon the earth, depend: clearly a goal within the possible attainment of the human faculties.

The primary elements of this doctrine I gave in Müller's Archiv, for the year 1838.* It was further developed by Nägeli.† Mirbel‡ dis-

* Schleiden, Botanische Beiträge, vol. i. p. 121.
† Schleiden und Nägeli, Zeitsch. f. w. B., vol. i. part 1.
‡ Sur la Marchantia polymorpha, Paris, 1831 et 1832, p. 32.

tinguishes three modes in which vegetable cells originate, which he terms "intra-utriculaire" (the process above descrived), "supra-utriculaire," and "inter-utriculaire." The first only of these modes is proved to exist by actual observation; the two latter have not been observed, and are gratuitous assumptions.

§ 46. According to Hugo Mohl*, another mode of increase obtains in the cells of the *Cryptogamia* (*Confervæ*), consisting in a circular constriction of the cell, which gradually advancing inwards divides the cell in the middle into two, so that a complete division of the cell into two new ones is effected.

These researches of Mohl contain the first and (except those of Nägeli and myself) the only actual observations on the multiplication of vegetable cells.† I have never been so fortunate as to observe a complete series of cells in this course of development, although I have frequently examined *Polysperma glomerata,* the plant which formed the principal subject of Mohl's researches. This has been the case also with Nægeli, who has explained the error in Mohl's supposition.‡

After Mohl, Meyen has been the principal advocate of this view, believing that he has in numerous instances recognised this process of spontaneous scission, and regarding it as almost a general law in plants. In most of the cases adduced by him, the fact has simply been invented, not observed. In the instance in which he refers to direct observation§ on the origin of four pollen-cells in the matrix, the fact is exactly the reverse; with reference to which, compare what is said on the subject of pollen in a subsequent part of this work.

Unger, also, has again propounded the multiplication of cells by scission as a general law in plants‖, but with as little truth as Meyen. Neither has he adduced a single instance in which he had actually observed the process of division. The fact that, in a particular instance, at first but one and afterwards in the same place two cells exist, that near one large cell two others occur which together perhaps have the same circumference as the first, does not throw the least light upon the process of multiplication: he has, however, no other facts to rest upon, or at least has not communicated them.

Whether cell-division occurs generally in plants is still to be determined. Certainly, the condition mentioned in the preceding section is the more frequent one.

## VIII. *Of the Termination of Cell-Life.*

§ 47. As soon as the play of chemical affinities has become impossible in a cell, the latter must be regarded as individually dead. So far, all cells must be considered to have died as individuals which

* Ueber Vermehrung der Pflanzenzelle durch Theilung. Tüb., 1835.

† To these names must be added that of Mr. A. Henfrey, whose original and interesting observations respecting the multiplication of vegetable-cells were first made known at the meeting of the British Association at Cambridge, in 1845, and have subsequently been incorporated in his work entitled "Outlines of Structural and Physiological Botany," Lond. 1847. Mr. Henfrey adopts Mohl's views with some modifications.—Trans.

‡ L. c. § Physiologie, vol. iii. p. 123, et seq.

‖ Bau und Wachsthum des Dicotyledonenstammes, Petersburg, 1840, p. 86, et seq.

have entirely consumed their contents, and contain nothing but air: the so-termed vascular, medullary, and liber cells; or those the contents of which have become converted into an isolated homogeneous matter, as the cells containing nothing but essential oil, resin, &c. The latter, however, are proportionately few in number.

Here we have another point, which has been either entirely neglected, or only superficially and cursorily treated of in books which for the most part do not even teach us any thing respecting the death of the whole plant. If we place the life of the cell wholly, or at all events for the greatest part, in the chemico-physical processes going on in the cell, we must term the cell dead in which these processes have entirely and for ever ceased. This is the case particularly in all cells which convey only air, which, being themselves dead, are saved from decomposition only by the living cells surrounding them, but which are instantly destroyed when exposed to the decomposing action of the atmosphere; as, for instance, the pith and heart-wood in trees becoming hollow, and cork and bark always at a certain time. There are, however, cells of this kind which gradually convert their whole contents into an isolated secretion, as into essential oil, as happens in the rhizomes of the *Scitamineæ*, in the leaves and stem of the Aloes, &c. In these cases the cell must be regarded as dead from that moment. The after-process is neither determined nor modified by the cell; it is a chemical process, and consists in the gradual oxidation of the essential oil, with the completion of which all farther change is at an end. It is in this way that the termination of the individual cell-life, even in the very interior of the most perfect plants, is indicated.

§ 48. Only the completely formed cellulose resists the usual solvent reagents; all the other substances of which cell-walls can consist, are still within the domain of the solvent or transmuting chemical forces which are active in the cell. All cells, therefore, whose formation is not completed admit of being again rendered fluid and becoming absorbed. This is the case in all mother-cells, in the spongy cellular tissue which originally fills the air-canals, in the nucleus of the ovule, &c.

It is undoubtedly a proof of superficial observation when a botanist, as has been the case, denies the resorption of organised structures in plants, an event which is observed with less facility in animals than in plants. The enormous number of mother-cells alone affords the most irresistible proof that this process does take place. But in what way it is effected is as yet unknown. Probably there takes place in this case a chemical change of the assimilated matter opposed to the formation of cellulose; that the former is first changed into jelly, then into gum (dextrin), and finally into sugar, and as such is absorbed. I would hereupon remark, that it has sometimes appeared to me as if, in the nucleus of the ovule, the cytoblasts reassumed a more sharply defined and younger aspect when their cells approached the period of solution. A peculiar transformation of already formed cells into an amorphous substance, "viscin," has been before adverted to (§ 12. 6).

§ 49. The life of the vegetable-cell continues only so long as the chemico-physical processes go on within it, and these become

impossible immediately that endosmosis is in any way arrested. The cell is then gradually destroyed by the action of the atmosphere, and decays, though in different ways as it is exposed occasionally or constantly to the action of water. The causes of this death may be various — laceration (as in the sporangia of the *Cryptogamia* on the escape of the spores), complete dryness, removal from the situation in which alone endosmosis is maintained (as in the fall of the leaf), &c.

The process of dissolution of a dead cell does not belong to Botany; we willingly commit the inquiry into it to Chemistry, and refer to the latest and best works on the subject, by Berzelius*, Liebig†, and Mulder‡. The causes, however, which expose vegetable-cells to these destructive influences are of interest to us; and we may name among them, as a very general one, the impossibility of endosmosis. Every vegetable-cell which can no longer take up fluid, in order to maintain the chemical processes within it, necessarily dies. Complete desiccation acts in the same way; and also the disruption of the cell, in consequence of which isolation of the materials contained takes place, and the processes going on within it cease. A peculiar state connected with this, is exhibited in most of the cells which are separated from a plant in the form of leaves. At the time of separation they are evidently not yet dead, for, under a very favourable though extremely rare conjunction of circumstances, a new process of vegetation may commence in one cell or another, in such a way that an entirely new plant is thence produced. Commonly, however, they die altogether, it being no longer possible for them to take up fluids, which had previously been brought to them in consequence of their connection with the entire plant.

## SECTION II.

### LIFE OF THE CELL IN CONNECTION WITH OTHERS.

§ 50. As soon as the cells are associated so as to constitute tissues, they exhibit certain modifications in their vital processes, and these modifications are especially worthy of consideration. Much of what relates to this part of the subject has necessarily been touched upon in former sections, as we are not yet sufficiently advanced to be able to comprehend with absolute precision the individual cell-life, and thus in many things that occur do not know how much or how little is due to the influence of the contiguous cells: much, also, that is undoubtedly referable to the combined action of several cells has necessarily been adduced, as serving to explain the nature of the individual cells. What we have now to consider are, first, the modifications which universally take place in the life of cells in consequence of their being associated; and afterwards, the special peculiarities incidental to the different tissues.

* Lehrbuch der Chemie, latest edition, vol. viii. † Organic Chemistry.
‡ Physiologische Chem. (Moleschott), p. 146, et seq. Translated into English, by Fromberg.

## I. *General Modifications of the Life of Cells in consequence of the Association of several Cells.*

§ 51. As soon as a large number of cells are united into a cellular tissue, part of them at least are shut out from immediate contact with the nutritive fluid; consequently, they receive nutriment by endosmosis only from the contiguous cells, in which, however, the fluid has always already undergone a change.

When all the cells of a tissue contain a fluid of equal density, endosmosis takes place in those which are in immediate contact with water, in consequence of which the fluid contained in them is diluted, and there is established between them and the next cells a condition of the fluids favourable to endosmosis, and so on. This is the most important relation in which cell-life can be viewed, because the sole, universal motion of the fluids, upon which the nutrition of the whole plant is contingent, arises therefrom. There are absolutely no vessels for the distribution of the nutritive fluid in the body of plants; and no person would take the trouble of looking for them, or would imagine he saw them anywhere, but one who goes to the investigation of plants labouring under the false and pernicious prejudice in favour of the supposed unhappy analogy between them and animals (§§ 63—146.). The sound sense of all botanists has been much confused on this subject; who have advanced every possible perversion of physics and logic, rather than part with this fixed idea.* Every living cell, however, which obtains fluid by endosmosis immediately induces in such fluid a chemical change and converts it into assimilated matter, so that the cells which are remote from the source of the raw nutritive fluid do not receive it in this state. In them, consequently, there is no occasion for the process of assimilation to go on, as far as relates to the decomposition of water and the fixation of carbonic acid; they enjoy, however, an active life, are nourished, form new cells, &c., as in the woody bundles of dicotyledons. This is sufficient to show how untenable is the law instituted by Liebig.†

§ 52. By the arrangement of a great mass of the cells in a plant, some of them are partially brought into contact with the atmospheric air. From this, two important conditions result: first, that the water evaporates constantly from the surface of the cell in proportion to the warmth, dryness, and motion of the air, unless the cells are protected in some special manner (§ 69.); in consequence of this evaporation the fluid in the interior of the cell is continually lessened in bulk and concentrated, and thus the endosmosis towards the other cells is strengthened and sustained: secondly, that the fluid contained in the cells is enabled to absorb gases from the air, viz. carbonic acid and ammonia, and occasionally oxygen.

* See Knight, in Treviranus's Beiträge zur Pflanzenphysiologie, Göttingen, 1811, p. 162. Sennebier, Physiologie végétale, vol. ii. cap. iv. p. 332.; and others.

† "No material can be regarded as the nutriment of plants whose composition is identical with or similar to their own, and consequently the assimilation of which can ensue without the separation of oxygen."—*Lieb. Org. Chem.* p. 26. The law is at once simply contradicted by the great number of *Fungi* and true parasites.

The conditions mentioned are of the highest importance as regards the life of the entire plant. Carbonic acid, ammonia, and water, constitute the chief nutritive matter of the cell, which, however, takes it up in various ways. Those cells which are in contact with fluid receive all the three substances at once. In this, consequently, must the most active assimilating process take place. Those cells which are partially in contact with the air obtain, it is true, on the one side, all necessary elements dissolved in water, but they can also receive, on the other side, carbonic acid and ammonia from the atmosphere. At the same time they give out into the atmosphere a larger or less quantity of water, by the loss of which their juices are concentrated, and this concentration again maintains the endosmosis. This enables us to explain how it is that after the bursting forth of their leaves plants no longer abound with such very watery sap, and yet continue the process of assimilation with greater energy. The perfect solution is conveyed farther by the endosmosis. The salts held in solution by the water and the inorganic constituents in general, upon which the chemical forces of the cell have little influence or none at all, are carried with the water unchanged through all the cells until they reach the surface of the cells at which evaporation takes place. At this point, they of necessity gradually accumulate in larger quantity, which accounts for the greater residue after incineration left by the leaves, green bark, &c. The water evaporated from the cell, like all water when evaporating, carries away with it a small quantity of non-volatile substances, on which account the water perspired by plants is never quite pure *, but is impregnated more with organic than with inorganic (less volatile) matter.

§ 53. By the association of many cells, and the reciprocal influence thence set up, certain modifications are produced in the life of the individual cells which have been in part previously considered. To these modifications is probably to be referred, in part, the formation of new distinct layers, and the spiral arrangement of the material constituting these layers connected therewith. This part of the subject also embraces the peculiar construction of air-vesicles between two contiguous cells, upon which the formation of the pores appears to depend.

What refers to this subject has been already discussed (§ 17.). In no isolated cell, in no cell previous to its association with others into a tissue, do we find spiral deposit-layers; nor, moreover, do we observe in any such the air-vesicles on the outer wall to which the canals of the pores correspond internally. It appears that the canals of the pores of two contiguous cells always correspond in such a way that they commence from an air-vesicle of this kind, or from a space in the common wall corresponding to it. We are acquainted with but few exceptions to this, which, however, demand further investigation. In *Juniperus Sabina* there occur in the bark thick-walled, four-sided, prismatic cells, the pore-canals of which regularly run only towards the four intercellular passages, which in this instance, and in a tissue which elsewhere presents no intercellular passages, appear to represent the air-vesicles above described. The same thing is seen in the parenchyma of the petiole in *Cycas* (vide p. 45.). In the epidermis-cells of several plants,

* Sennebier, Phys. vég. t. i. p. 79., and many others.

as, for instance, in *Cycas* and *Abies*, pore-canals also find their way towards the free surface (vide pp. 45—50.).

§ 54. Peculiar changes also take place in the secretions, the more solid secretions assuming definite forms. To these may be referred the gelatinous envelop of many *Algæ;* the intercellular substance, the peculiar matter, which invests the spores and pollen-grains; and the matters secreted from the epidermis.

Most *Confervæ*, several *Ulvæ*, &c., secrete a large quantity of gelatinous matter, which assumes a definite form, and thus frequently determines the figure of the whole plant, as in *Chætophora* and *Undina*. In most *Confervæ* it constitutes a delicate uniform membrane investing the whole plant; in *Rivularia*, *Chætophora*, *Nostoc*, &c., larger masses. It is always wanting, however, in the spore, and is not formed except by the vital activity of the self-multiplying cells.*

In the same way a solid substance is secreted in the intercellular passages: a similar secretion, of determinate form, is also found on the epidermis. The subject of both these secretions will be entered upon more fully hereafter (§ 59. 63.).

The most interesting and most complicated phenomenon, however, still remains—that of the peculiar investment of the spores and pollen-grains. All spores (except those of the *Algæ*, many *Fungi*, and some Lichens), all pollen-grains (with the exception of those of plants which flower under water), are constituted of the proper, essential cell, which is formed as such, and a peculiar material investing it, which is simply uniform or is furnished with warts, protuberances, spines, bands, or the most extraordinary abnormal formations, disposed irregularly or with the utmost mathematical regularity. The nature of this material differs from all known assimilated vegetable substances in this respect: that it is affected, according to Fritsche, not at all, according to others but very slowly, by concentrated sulphuric acid, but is always rendered more opaque, and sometimes of a purple-red colour. The matter itself presents various colours, mostly yellow, though also blue, red, green, brown, &c. It is a pure product of secretion of the spore, or pollen-cell. I shall be obliged to say more about it afterwards, when speaking of the pollen. For our best information respecting its chemical nature, but especially with respect to its extraordinary forms, we are indebted to the indefatigable and astonishing researches of Fritsche.† Mohl's ‡ opinion upon this point—that the external pollen-membrane is intercellular substance, in which perfect cells or their beginnings (as granules) are formed—appears to be completely contradicted by Fritsche's, Meyen's §, my own, and Nägeli's ‖ investigations. The peculiar chemical nature of the material appears at once to be opposed to any comparison of it with the substances of which cells are formed.

§ 55. The peculiar relation in which the sap-currents stand

* This condition has not been quite correctly comprehended by Mohl, Erläuterung und Vertheidigung meiner Ansicht von der Structur der Pflanzensubstanz. Tübingen, 1836. In other respects he shows, as usual, distinguished powers of observation.

† Fritsche, Ueber den Pollen. Petersburg, 1837.

‡ Hugo Mohl, Beiträge zur Anatomie und Physiologie der Gewächse, Part I.; und Erläuterung und Vertheidigung, &c., p. 18. and elsewhere.

§ Physiologie, vol. iii. p. 146, et seq.

‖ Zur Entwicklungsgeschichte des Pollens, &c.

towards each other in their direction, in two contiguous cells, manifestly depends upon the association of the cells, since in the *Charæ*, without exception, the current in the one cell corresponds to a current in an opposite direction in the other.

The fact itself is indubitable, and is readily observed in *Chara*, and partially also in *Vallisneria*, &c.: the reason of it is wholly unknown. It shows, however, pretty distinctly, that the necessary conditions of the sap-motion lie altogether or in part *external* to the cell, and that endosmosis probably has a great share in producing them. We never observe, also, in cells which are in contact with others on all sides, as in *Najas* and *Vallisneria*, that the currents cover the whole of the walls, but exist only on two opposite sides, which lie, throughout all the cells, in parallel planes, by which the possibility of the contiguous streams being frequently in opposite directions throughout the plant is explained. The second kind of sap-motion in a network of minute currents is probably connected with a greater degree of independence and disconnection of the individual cells among themselves; and it is also but very rarely observed in the closed cellular tissue.

§ 56. The individual cell may, as regards its own vital processes, be already dead, but yet retain its connection with other living cells, and probably also conduce to their vitality, and consequently to that of the whole plant, for some time longer. In this way, probably, the so-called vessels, at the period of the ascent of the sap in spring, are reservoirs for the reception (quite passive) of the superabundant sap, which is not yet fit for assimilation; but at other times they are receptacles for secreted air: the same with the cells which contain special secretions, &c.

It is a peculiar condition, and one proceeding only from the high degree of individualisation of the cell, and its association with others into a plant without complete abolition of its own individuality, that it may be so circumstanced as relatively (to itself) to be dead, but, as regards the whole plant, still to be deemed alive. This condition also shows how futile and inapplicable all analogies between animals and plants are,—two creations, whose most intimate nature is so entirely different, that almost every comparison proceeding upon the constitution of the elementary organ is a mere delusion of the fancy, without any scientific value.

## II. *Peculiarities in the Life of entire Tissues.*

§ 57. It may be stated generally, that the vital processes in each individual cell in the same tissue are identical, or at all events very much alike: thus, similar elements frequently compose the greater mass of the parenchyma; the alburnum-bundles, the milk-vessels, &c. of a plant, contain the same substances. Important exceptions, however, are also met with; and we find in the parenchyma, and in closely contiguous cells of the same form, contents of very different nature; and in the vascular bundles and elsewhere

the different vital properties of the individual cells are exhibited in the varying mode and rapidity with which the cells themselves are perfected.

It can only be regarded as a law having an average or general application, that the cells of an entire tissue have identical functions; and such important exceptions exist in this respect, that the classification of the tissues, according to supposed differences in their functions, appears to be at least wholly untenable; the morphology of the cell alone affording a sufficient principle to go upon. In the same parenchyma we find a cell crammed full of starch, next to a similar one containing nothing but essential oil; and both, probably, contiguous to a third, filled with a clear, watery, red or blue coloured matter; whilst a fourth, together with various assimilated substances, contains a large quantity of chlorophyll. In the midst of the thin-walled parenchyma we observe scattered, or forming groups with the others, cells of the same size and form, but filled up almost to the closure of their cavity by deposit-layers, as in the so-called stony concretions in the quince and pear, in the bark and pith of *Hoja carnosa*, and of many trees, in the aerial roots of the *Maxillariæ*, and in a hundred other situations. All this indicates the great independence of the individual cells, and the possibility of each cell, in any situation, on occasion, going through all the phases of cell-life, and becoming developed in any way that the circumstances under which it is placed render necessary. The cell-life is modified only to a slight degree by the mode of disposition of the cells, and consequent dependence on the contiguous cells. Leaving this independence out of the question, the tissues, as a whole, present certain phenomena which must be regarded as peculiar to each.

§ 58. The cells of the parenchyma enjoy the greatest degree of independence, and it is, consequently, in that tissue that we find, in the greatest number and disposed with the least regularity, cells with the greatest variety of contents, and having the most various configuration of their walls, next to each other. Larger masses of the parenchyma present, in preponderating quantity, starch (potato), or fixed oil (cotyledons of the species of *Brassica*), or gum (roots of *Althæa*), or emulsin (oil and vegetable albumen in the cotyledons of the almond), or assimilated substances and chlorophyll (in all green leaves), or colouring matters of the same kind (in the petals of flowers), or air (in the pith), &c.

§ 59. The various formations in the system of intercellular spaces comprehend a very great variety of substances. The peculiarity in this case consists in the circumstance, as I believe, that all the cells forming the boundaries of these intercellular spaces, without exception, exhibit equal vital activity; they either exert no influence at all upon the contents of the intercellular spaces, or all secrete into it the same material. To this system are to be referred all the various reservoirs of special secretions, resin- and gum-passages, as well as the receptacles of the milk-sap; and, besides these, the solid intercellular substance (*substantia intercellularis*), which frequently presents a determinate form, dependent on the neighbouring cells.

Respecting the process by which the reservoirs of proper juices are filled with the matters contained in them, the preparation of this matter by the neighbouring cells, and the power through which these materials are secreted within the reservoirs, we as yet know nothing. All these particulars being left out of consideration, the only differences presented by the intercellular spaces, which are filled with a solid substance, arise from the nature of the secreted substance. These spaces present two varieties of form. In the wood of dicotyledons, and in other instances, the narrow intercellular passages are frequently occupied by a substance homogeneous in appearance, its colour and tenacity differing in some degree from those of the cell-wall.

On the other hand, the constitution of the intercellular substance between the cells of the external cortical layer in the *Chenopodiacæ*, *Amaranthaceæ*, *Umbelliferæ*, *Malvaceæ*, &c., is more remarkable.

If we examine these cells in a transverse section of *Abutilon graveolens* (fig. 99.), we observe large intercellular spaces formed by from three to six cells (*b*). From each of the cell-walls, forming the boundaries of the space, there projects into it a semi-solid, semi-gelatinous mass (*a*); the aggregate, however, of these masses is not sufficient to fill up the whole intercellular space.

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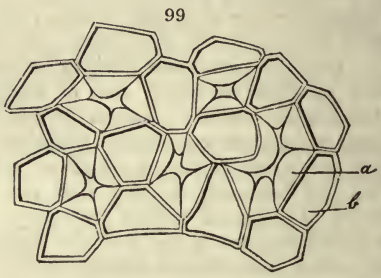
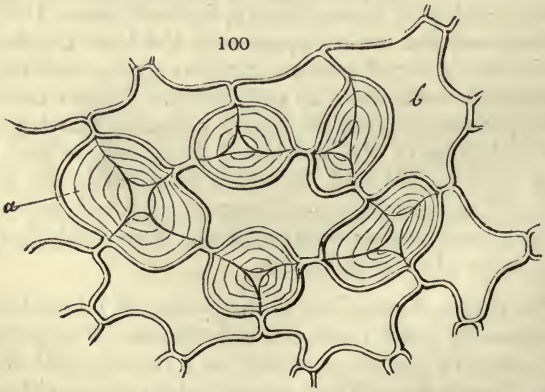



In *Amaranthus viridis* (fig. 100.), three cells on a transverse section present a stellate form (*b*), and in this way constitute very spacious,

100




rounded, intercellular passages, which also are partially filled with a secreted substance (*a*), exhibiting concentric laminæ, which run parallel

[99] Transverse section from the outer cortical layer of *Abutilon graveolens*. *a*, The intercellular substance secreted by the cell-walls. *b*, Cells.

[100] Transverse section of the outer cortical layer of *Amaranthus viridis*. *a*, The intercellular substance secreted in laminæ by the cells.

to the cell-walls from which they are secreted. The latter circumstance appears to me to be decisive of their nature as a product of secretion.

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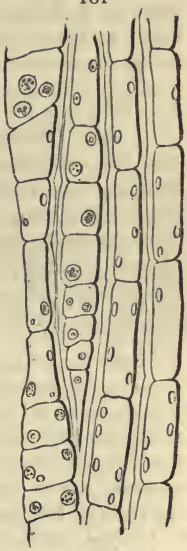

Lastly, upon examining the same formations in *Justicia carnea*, in a longitudinal section (fig. 101.), the secreted substance is seen to be continuous throughout the whole length, between the rows of cells, and presenting only indistinct traces of division.

The history of the development of these formations is at present deficient. Mohl's * earlier opinion, according to which the intercellular substance is said to be the remains of the primordial material in and from which the cells are formed, I consider decidedly incorrect, and to be contradicted by Meyen's † discovery of the division into portions of the intercellular substance. He has himself also, perhaps, since then relinquished this notion.

It appears, however, to me that, to the above described formations in the external cortical layer in the families mentioned, and some others, other different but analogous forms must be referred, particularly the cells of the cotyledons in *Schotia speciosa* and *latifolia*, *Tamarindus indica*, and some other *Leguminosæ*, as well as the very similar formations between the angles of the epidermal cells in many species of *Begonia*, and of the leaf-cells in several *Jungermanniæ*. In these instances, also, a triangular intercellular space appears to be filled with a substance secreted from the three cells forming its boundaries, as has been also observed by Meyen ‡ in *Begonia*. Of some formations (particularly those in *Schotia* and *Jungermanniæ*), Mohl has now offered an explanation similar to that which he gives of the secreted layer in the epidermis, viz., that the cells are thickened by a laminated deposit on the internal surface, in consequence of which the outer layers must necessarily constantly undergo a change in their chemical nature, for in all these formations the apparently perfectly *continuous* cell-membrane bounds the cavity of the cell. How far Mohl is inclined to extend this view of his to other conditions, I know not. I must confess, that the view propounded by Meyen at present appears to me to be inadmissible. As yet, however, a complete history of the development of these structures is wanting, to enable us to arrive at a more certain conclusion.

The semi-fluid gelatinous matter which occurs in the intercellular spaces of the albumen of the *Cassiæ* and other *Leguminosæ*, between the cells of the Lichens, especially of the utricular layer, but, above all, in the intercellular spaces of the *Fucoideæ*, which latter very nearly approaches dextrin (?), presents a manifest transition from the

* Erlauterung und Vertheidigung meiner Ansichten über Pflanzensubstanz, &c.
† Physiologie, vol. i. p. 170. ‡ L. c.

[101] Longitudinal section through the outer cortical layer of *Justicia carnea*; perpendicular rows of cells with chlorophyll granules, intercellular substance, secreted on both sides of the intercellular passages.

intercellular substance to gum. The cells are occasionally observed to exist previous to the formation of these matters; and the latter are found to increase, instead of diminish, on the completion of the cellular tissue; consequently they are in all probability secreted by the cells.

§ 60. All the cells of the vascular bundles exhibit nearly identical vital processes, and differ for the most part only in their age and the configuration of the walls dependent upon their age. The vessels, when completed, convey air, and perhaps admit juices, but these only occasionally for a short time, and in any case passively. The other elongated cells of the prosenchyma exhibit, as long as the tissue is living, a rapid change of matter in their interior, and, consequently, in general contain a homogeneous watery fluid. They subsequently lose their vitality, and then convey nothing but air.

That the vessels convey only air, and no juices, may be seen by any one, possessing the least physical knowledge, on the most cursory glance at a longitudinal section of a plant. That any dispute should have arisen on this point, only shows how exceedingly confused most observers are by prejudices and supposed analogies: it is not worth while, however, to waste words about it. It has been already remarked (pp. 57, 64.), that the cells of the vascular bundles probably owe their elongated form itself to a rapid current through them of the sap in a determinate direction, by which means their extremities are more vigorously nourished than their sides. This rapid change explains the circumstance of the chemical processes carried on in them being very simple. We very seldom find peculiar substances formed in them as long as they retain their vitality: even the more solid assimilated matters, as starch, occur in them but seldom, and in small quantity. When they have begun to lose their vitality, however, (to constitute heart-wood,) they for the most part cease altogether to convey sap; and where they are not completely protected against the external air and moisture, a process of chemical decomposition (decay) is set up, in consequence of which, although retaining their form, they are gradually converted into substances rich in carbon. The peculiar products of the wood, tannin, extractive matter, colouring matter, probably for the most part owe their origin to this process; less frequently to the sap-channels, bounded by parenchymatous cells, which penetrate the wood, as is the case with the resinous products in the *Coniferæ*. This subject, however, still presents an extensive field for further investigations.

§ 61. With regard to the peculiar vital properties of the liber-cells, of the usual form, as seen in the *Apocynaceæ* and of the milk-vessels, our knowledge is equivalent to nothing at all. Every thing with respect to these remains to be investigated.

On the subject of these structures, and especially on the milk-vessels, I am rather afraid of saying too much than too little, for, owing to the total neglect of a correct, scientific method, and the puerile sporting with hypotheses, without any foundation or guiding principle, the question respecting them is loaded with such a heap of nonsense, that the best way in beginning upon it is, in the first place, to throw overboard all that has hitherto been done and commence entirely *de novo*, instead of undertaking the thankless task of cleansing this true Augean stable.

In the works of our first botanists we meet with such propositions as this: — "The vessels of the stem which belong to this system are the expressions of the two foci of the ideal *ellipse* of the true peripheric circulating system. The one abside conducts towards the light, .... the other abside carries the diagonal of the former in an opposite direction into the darkness. . . . ." Words like these are so entirely without meaning, that one scarcely knows what to say to them. But when once the reins of a sound method are broken, there is no stopping short of the most absolute nonsense, the writer not even having the least suspicion of it. Almost every page that has been written on the milk-vessels exhibits proofs of superficial observation, unbridled fancy, unscientific physical notions, &c. The whole idea of a universal intercommunicating system of vessels throughout the plant ("a cell with multifarious ramifications through the plant, but closed in itself," Meyen) is purely visionary (how could the few little sections, taken from a plant upon which observations are made, afford foundation for a notion of this kind?); but writers have been so deeply smitten with it, as to have adduced it as the fruit of observation with the utmost coolness. Up to the present time, a motion of the milk-sap has been noticed in only two or three uninjured plants; and even in these instances only by the direct light of the sun, observations made with which are so open to optical illusion: from them, however, a universal circulation is boldly deduced, and its direction, even through the entire plant, described with the utmost precision. The escape of the sap from cut portions is viewed as a decisive proof of its motion in the uninjured part. Does not the wine in a cask also move as it runs out, when the tap is turned and the equilibrium which had hitherto existed is destroyed? "The sap is expelled only by a vital action, otherwise it would be retained by capillary attraction," say others. But do those who make this assertion know what capillary attraction is? Unyielding walls are essential to it, but not thin membranes in a turgescent tissue. Do they know how capillarity acts? — that it exhibits a determinate relation to the size of the tube, the nature of the material of which the tube is composed, and the mutual relations of the fluid and tube towards each other; and also that it exists as capillary *elevation* or capillary *depression?* Have they measured the diameter of the latex-vessels, and determined the capillary force of the substance composing the tubes and of the fluid, and from these data calculated their capillarity? Oh! no, — it is much easier to weave vain fancies than to make accurate measurements and precise calculations? What is the amount of the flow, then, from a stem when cut across? Very little; and it is necessary to make a fresh section to procure another flow of sap, and so on. In this case it would not be wholly improbable that the capillarity should actually retain some of the sap after the escape of that portion of it which could not be thus retained. But in every case, however the escape is effected, leaving out of view the actual motion of the sap in uninjured plants, by the turgescence of the contiguous cellular tissue; and this cause must always be first taken into account. It explains, for instance, very readily, the reason why more sap escapes from the upper end of a cut stem than from the lower; because the younger cells, with more yielding walls and more distended with fluid, must necessarily enlarge more than the more closely united, older, and thick-walled cells in the lower portion of the plant. Arguments of this kind might be multiplied to a great length, but what I have observed is sufficient to show how very superficially this subject has been treated. It is by no means my intention in this way to prove the non-

existence of the motion of the latex, but merely to show that the mode in which this subject has hitherto been treated cannot lead to any useful scientific result.

When the facts themselves are consulted we must accurately divide them into two sets; those which are derived from the prepared, and those from the uninjured, plant. It must, moreover, here be remarked that in the very young condition only a clear watery fluid is contained in the latex-vessels, and consequently that it is impossible to observe any motion in it; and that in vessels of a certain age, and with thick walls, the latex coagulates in many ways, and is transformed into a solid mass, as, for instance, in the *Euphorbiacæ*. The question respecting a motion can only arise principally with respect to vessels of an intermediate age. Under these circumstances, when a section is placed under the microscope, a rapid motion is noticed in the, for the most part granular, sap *, frequently in opposite directions. Upon looking at the extremities of the cut vessels, a protruded and coagulated mass will be found at each end of the same vessel, and at the same time an outward current will be remarked at each side or the commencement of such a current at one side; and when the escape of the fluid is stayed at this point by the coagulum, immediately after its cessation, an outward current will be established on the other side: so that it is impossible, without a preconceived notion, to regard *this* motion as it appears in *these* observations as one having a determinate direction.

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In uninjured plants, the motion of the latex can very seldom be successfully shown: even in *Chelidonum majus* it is only occasionally possible, and then presents great optical difficulties. It is easy, on the other hand, to observe it in *Alisma Plantago*. In this case a motion is undoubtedly visible, viz. a current sometimes more rapid, sometimes slower, and, in the same vessel, sometimes in one direction, sometimes in the other, but frequently alternating with very long periods of quiet. Of a regular motion in a determinate direction, I have never been able to observe any indication. What I have just stated, then, may in general terms be said to include all that I have been able to arrive at as a certain result, from the most careful observations made on the most different

* Meyen, who at one time saw cells everywhere as *Muscæ volitantes*, also regarded these granules in the same light. They are, however, decidedly consistent, solid granules.

[102] Latex-vessel from the leaf of *Limnocharis Humboldti*. At the commencement of the observation, the upper end (*a*) emptied itself and collapsed. The arrows indicate the observed direction of the outward current. Every latex-vessel is bordered by two rows of narrow, somewhat elongated, parenchymatous cells (*b*).

plants, and under the most varied circumstances. Every one having the slightest idea of what experiments, hypothesis, induction, and theory really signify in the natural sciences, will certainly agree with me, that, in the generally defective state of our knowledge respecting the physical and chemical processes going on in plants, it would be altogether a childish undertaking to attempt to weave a theory out of elements such as these ; and any others are, as yet at least, in dispute. Let any one that will have recourse to the convenient scape-goat of a universal vital power amuse himself with it, but he must not imagine that in doing so he is proposing any thing profound or really scientific. It is also clear that we have no certain facts sufficient to afford foundation for an analogy with the motion of the blood in animals, even allowing that this analogy is any thing more than an idle and fanciful notion.

Respecting the contents of the latex-vessels and of the other two forms we know just as little. They differ specifically in almost every plant, and frequently in different individuals of the same species, at least in the quantity of the separate constituents. It would appear that the latex pretty generally contains caoutchouc in granules, in greater or less quantity according to the age and the manner of vegetation of the plant. It also presents a great number of peculiar substances, for the most part of a poisonous, at all events of a highly suspicious, nature. Of the contents of the liber-cells we know nothing at all. With regard to the importance of the latex, in respect to the life of the plant, if we disregard Schultz's wholly unfounded fancies, we are also entirely in ignorance. Meyen *, after collecting all the cases in which the latex is innoxious, and showing that, in many instances where it is poisonous, innoxious substances are also found in it, concludes "that the latex *may* be a thoroughly elaborated nutritive juice, at least as regards man and animals, and *therefore* the assumption that it also plays the part of a nutritious sap in the plant is certainly not inadmissible." It is certainly impossible to arrive at a conclusion more illogically. Commencing with the absolutely poisonous latex of *Antiaris toxicaria*, *Hippomane*, and *Excœcaria*, when it is shown how frequently an innoxious latex, as, for instance, that of the young lettuce, becomes poisonous as soon as the plant is only in some degree perfected, how the poppy can be poisoned with opium, and the lettuce with lactucarium, there would appear to be much better reason for arriving at an exactly opposite conclusion. But, on this subject, the question is not at all as to inferences and conclusions ; we have here to deal only with suppositions and assertions.

Probably all these organs, like the latex receptacles by which they are frequently replaced, are for the purpose of receiving matters, and preventing their reaction upon the living cells, which would otherwise be detrimental to the life of the plant. This is at all events indicated by the circumstance that almost all vegetable poisons, and which act as such on the very plants by which they are yielded, are found in the latex ; but, as yet, nothing but the most vague suppositions can be broached. Liebig's † notion, that in plants with a milky sap the water is surrounded by an impervious case of caoutchouc, and that plants in a hot climate are thus secured against desiccation, arises from a complete ignorance of vegetable structure.

* Pflanzenphysiologie, vol. ii. p. 410.

† Organische Chemie, p. 57.

§ 62. Of the filamentous tissue of *Fungi* and Lichens we know at present next to nothing. The cells usually contain a clear colourless juice; in the Lichens, occasionally, air.

§ 63. The epidermal cells contain a clear aqueous or coloured fluid, rarely here and there peculiar substances, as resin (in *Aloe nigricans*). Externally the true epidermis affords peculiar secretions, at first a waxy material, usually in the form of a delicate layer, which renders the surface smooth or shining, more rarely in that of minute granules (the so-called *bloom*, *pruina*), in either case protecting the epidermis against being wetted or penetrated by water, thus rendering all interchange of gases and vapours impossible excepting only through the stomates. A second layer (*cuticula*) is subsequently formed beneath this first secretion, which is composed of an assimilated material not yet precisely investigated. This layer is in many cases of great thickness, and constitutes tubercles, warts, and such-like productions, especially in the neighbourhood of the stomates. In their vital properties these epidermoidal appendages exhibit numerous varieties, and in them again we meet with very various contents and peculiar secretions. With respect to cork, we only know that it soon dies and decays bit by bit.

The epithelium differs from the parenchymatous cells only in its clear aqueous juice: the epiblema has not as yet been sufficiently investigated. But as soon as the epithelium is converted in the *air* into epidermis, it becomes covered with a delicate layer of a material which can be removed by absolute alcohol or ether, and which always gives the epidermis a certain brilliancy, and affords a perfect protection against its being wetted by water: the latter is the most important point. We well know that a membrane penetrated by moisture offers no impediment to the evaporation of the water enclosed by it, and to the absorption and transmission of gases, but that the contrary is the case with a dry membrane. In this way the epidermis isolates the cells of the parenchyma from all action of the atmosphere, as, owing to the intervention of the epidermis, they cannot receive anything from it nor give out anything to it. The whole reaction, therefore, is limited to the stomates, through which alone is evaporation or interchange of gases possible. This peculiar investment of the epidermis has been hitherto wholly unnoticed, and has been recognised only in those cases where it is presented in greater quantity, in the form of minute granules, as the "bloom:" it exists, however, on every epidermis, and may be removed by ether, when the cells of that membrane, like all others, become permeable to water.

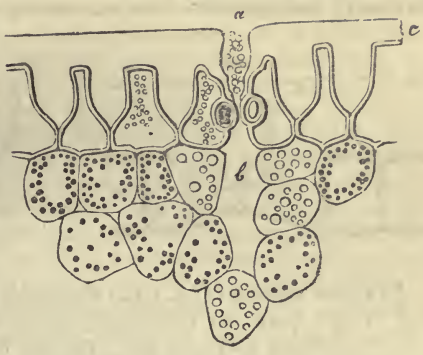
In a section perpendicular to the surface this waxy secretion can be demonstrated only in those cases in which, as in *Elymus arenarius*, *Strelitzia farinosa*, &c., it attains a considerable thickness: consequently it is not shown in all the woodcuts appended to this Section.

The object of preventing, by this layer, all evaporation, &c. on the surface of plants is probably still further promoted by the secondary secretion.

Upon examining a fine transverse section of the epidermis of *Aloe*

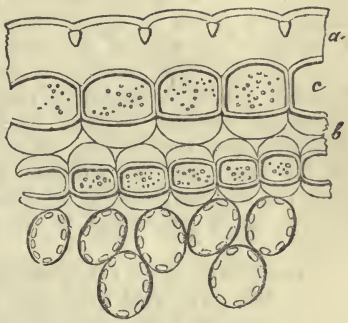
*nigricans* (fig. 103.), epidermis-cells enlarged outwardly into papillæ will be observed, although the surface of the leaf is very nearly smooth, the spaces between the epidermis-cells being filled up by a material which extends outwardly far beyond them, is readily distinguishable from the cell-membrane by its optical properties (fig. 103. *c*).

103




When a very young leaf of *Hyacinthus orientalis* is inspected, it will be seen to be enveloped merely by a delicate epithelium, the cells of which are slightly elevated on the external surface in a vesicular manner. During the further development of this epithelium a gelatinous matter appears first in the depressions between the cells, which soon hardens, and thus represents a network, the meshes of which indicate the limits of the cells. In a short time the cells are wholly covered with a similar layer, which is firmly united with the network above described, and which, also, rapidly hardens. The epidermis-cells now secrete on their external surface a material of less consistence and density, which raises the former layer, together with the fibrous network, and gradually attains considerable thickness.

104



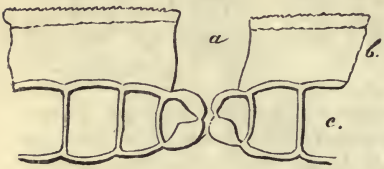

These distinct portions may be observed even in the completely-formed cuticle of *Dipsacus fullonum* (fig. 104.) But in this instance the epidermis-cells (*c*) secrete this layer, not only on their external aspect (*a*), but also secrete an intercellular substance on their internal aspect (*b*); and in this respect the same condition obtains in the layer of cells immediately subjacent to the epidermis.

[103] A section perpendicular to the surface of the leaf of *Aloe nigricans*. *a*, Canal of the stomate, filled with orange-coloured granules of resin. *b*, Cavity beneath the stomate, surrounded by cells, containing in part chlorophyll granules (black in the figure), and in part rose-red or orange-coloured resin granules. The papillary cuticular cells are filled with fluid of a brighter or darker red, and in part with rose-red resin granules. Of the two cells forming the stomate, the one contains chlorophyll, the other a single large bright-yellow granule of resin. *c* is the secreted layer of the epidermis-cells.

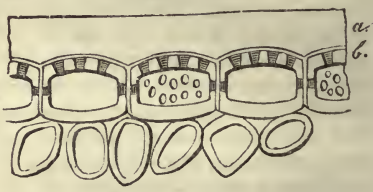
[104] A section perpendicular to the surface of the leaf of *Dipsacus fullonum*. *c*, The epidermis-cells, with their granular contents. *a*, The secreted layer of the epidermis cells, on their external surface. The most external portion of this secreted layer is more dense, and readily distinguishable; beneath it, and corresponding to the furrows between the cuticular cells, is a fibrous network, also composed of a more dense material. The epidermis-cells also secrete from their internal surface an intercellular substance, which, in this situation, joins that which is secreted by the subcuticular layer of cells, which cells are again covered, on *their* internal aspect, with an intercellular substance, resting upon the more lax green parenchyma.

The cuticula (*b*) is remarkably thick in the Tree Carnation (baumnelke) (fig. 105.), in which the first and firmer secretion can also be clearly distinguished from the subsequent and softer deposit.

105




106




In *Cycas revoluta* (fig. 106.) the entire secreted layer is homogeneous; but in this plant an interesting condition is presented, the epidermis-cells exhibiting pores on the external wall, in consequence of which it is more easy to distinguish the membrane of the epidermis-cells from the secreted layer.

Hugo Mohl * has furnished a whole series of other peculiar modes in which this secreted layer is formed.

Sometimes the first secretion is formed more prominently in definite situations; for instance, on the middle of the cell (*Phormium tenax*), or at two or three points, or at the margins of the stomates (*Agave americana*), constituting warty and other similar productions. It is frequently deposited so irregularly that it appears as if scratched with needles, as in *Epidendrum elongatum*. In most cases the secretion manifestly differs in aspect from the outer wall of the epidermis-cells. Frequently the wall of the cells merely appears to be thickened; but, even in this case, careful maceration will render the secreted layer evident, which is elsewhere readily seen. It is in this way that the membrane termed *cuticula* by Brongniart is obtained.† Along with this secretion, that of the waxy substance is also probably developed; for the more brilliant and less pervious to water, and the less readily deprived of that property by means of alcohol, do we find the epidermis cells to be in proportion to the greater thickness of the last-described layer.

I must here, however, mention two different views that have been more lately advocated respecting the layer of secretion on the epidermis. The former has been developed by H. Mohl in the Linnæa (1842). He is of opinion that the secreted layer is wholly formed from the outer walls of the epidermis-cells, which become thickened in the usual laminated manner, and, in fact, in such a way that normally the innermost last-formed lamina acquires the nature of the original membrane, whilst the exterior older laminæ become gelatinous, or otherwise variously modified by the common membrane. This view is based upon very precise and comprehensive investigations of the *perfect* epidermis, to which

* Linnæa, 1842. † Annales des Sciences natur. tom. xxi.

105 Perpendicular section through the epidermis of the leaf of a Tree Carnation. *c*, Epidermis-cells covered with the secreted layer (*b*), which, externally, is constituted of a more dense deposit. *a*, Passage through the secreted layer to the stomate.

106 Section perpendicular to the surface of the leaf of *Cycas revoluta*. The epidermis-cells (*b*) are porous on the lateral and external aspects, and, on the latter, covered with the secreted layer.

Mohl very briefly adds the remark, that the development is also in accordance with it. I believe that a thoroughly complete history of the development of this structure would have been on all accounts of greater importance than the most comprehensive observation of it in its completed state. I believe that H. Mohl will be obliged to admit with me that all the completed forms may, in the absence of any preconceived opinion, be explained at least as well according to my view. I believe, however, that his mode of explaining this formation is met by insuperable difficulties in certain conditions, as, for instance, in *Cycas revoluta* on account of the formation of the pores, which elsewhere universally proceeds from the original cell-membrane. By far the most simple and most natural explanation of this formation in *Cycas* appears to be the following: that on the one side (externally) a secretion has been deposited, and on the other side (internally) a thickening of the original cell-membrane has been effected by the formation of laminæ, up to the commencement of the pore-canals. In this case, also, the observation of earlier conditions shows that the pores become visible at least simultaneously with the commencement of the formation of the "cuticula," and probably even somewhat earlier; a fact that is totally irreconcilable with the view advocated by Mohl. I must continue, for the present, to consider my view as supported by the observation of the course of development of the secreted layer. Especially do the observations on *Oryza sativa*, the Hyacinth, and on *Dipsacus fullonum*, appear to me to afford sufficient assurance of its being well founded.

The second view has been proposed by Hartig (Beiträge zur Entwicklungsgeschichte der Pflanzen, 1843). He assumes that the first cell, the foundation of the whole plant (primary cell), remains persistent, and envelopes the entire plant, continuing to grow during the whole life of the latter; that it is sometimes drawn through the stomata into the intercellular spaces, and is sometimes continuous over the stomata, closing them up.* This primary cell subsequently acts like all other cells; that is, it secretes, as "ptychode," an "astathe," and "eustathe," which would appear to be my "secreted layer," the history of the development of which is given with perfect correctness, and accords with mine. With respect to this it is to be remarked, that, in direct opposition to his entire view of the mode of formation of cells, Hartig in this case assumes that the "eustathe" is formed *before* the "astathe;" moreover, although a secretion may be allowed to take place in the case of cells with amorphous contents, in which chemical changes are proceeding, it cannot be admitted to occur in Hartig's imaginary primary cell, which has no proper contents at all, but merely encloses the cells of which the plant is constituted. Consequently, in this case the epidermis-cells must have secreted exteriorly their proper "eustathe" and "astathe," and then, by means of these and the "ptychode" of the primary cell throughout, also the "eustathe" and "astathe" of the primary cell. It will, from what precedes, be already evident that this view is very obscurely worked out, and consequently cannot in any way be derived from direct observation. Moreover, it is again to be remarked that the existence of the primary cell in the form of a membrane immediately superjacent

* This double relation of the *cuticula* to the stomate is of itself in the highest degree improbable, and is evidently only imagined in order to bring into accordance with the notion set up by him of the primary cell the incontrovertible fact that the stomate, for the most part indubitably open, leads into the subjacent intercellular space.

upon the epidermis-cells is not proved by Hartig in a single actual instance; and proof is also wholly wanting, that the delicate "cuticula," rendered evident on the embryo by sulphuric acid, is identical with the presumed "ptychode" of the primary cell lying immediately upon the epidermis-cells, and much less with the outermost secreted layer (the "eustathe") of the epidermis-cells. I consequently consider the view which I have developed, and which is not, as Hartig says, the general one, but peculiar to myself, to be, as yet, the better founded and more correct of the two.

The two cells of the stomate do not differ, as has been previously remarked, in their contents and vital properties from those of the subjacent parenchyma. The width of opening of the fissure left between them varies at different times, and in different parts in the same plant; and it is thence evident that the degree of admission of atmospheric air to the parenchyma is variously modified. Our knowledge with respect to these cells is, as yet, very imperfect, and we do not even know whether the contraction of the fissure be effected by the turgescence or by the collapse of the cells. The latter appears to me to be the more probable supposition, because when the evaporation is too rapid, in which case these cells are evidently the first affected, it would by this means be checked.

The appendicular organs, again, consist of cells, which, like the parenchyma, have necessarily relinquished less of their individuality, owing to which innumerable peculiar processes continue to be exhibited in them, the production of special substances, some of which are secreted, particularly viscous, saccharine, resinous matters, and essential oils. The conditions exhibited in these organs are endlessly multifarious, and what is necessary regarding them has already been partly referred to.

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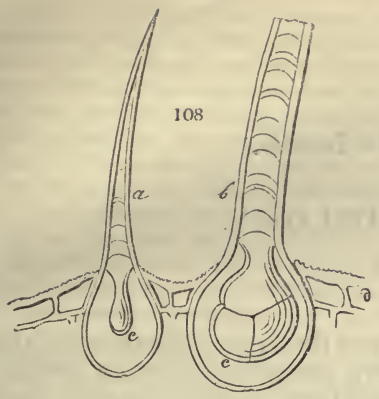
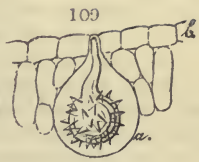
To one phenomenon, however, I must here direct attention. The stinging hairs of the *Boraginaceæ* (*Borago officinalis*, fig. 107.) and *Urticaceæ* become filled, when old, from the point towards the base, with an assimilated material deposited in laminæ, and differing from the wall. In the *Urticaceæ* (in the *Boraginaceæ* I have not as yet been able to observe any thing similar), this deposit, when it has extented to the dilated base of the hair (fig. 108. *c*), constitutes a globular mass projecting into the base of the hair, the peduncle of which is sometimes longer and sometimes shorter (*Ficus*, *Broussonetia*), and which is occasionally beset with minute crystals of carbonate of lime (fig. 109.). In *Cannabis* a minute point only of these hairs projects above the epidermis; in *Urtica canadensis* there is merely a large globular cell, level with the surface of the epidermis; in *Parietaria judaica*, *Humulus*, *Forskœhlia tenacissima*, a similar cell (*a*) is placed beneath the epidermis (*b*). I believe the latter might be regarded as stinging hairs, normally undeveloped in accordance with a specific law.*

* Meyen (Müller's Archiv, Jahrg. 1839, p. 257.) discovered these concretions in *Ficus*. Payen (Froriep's Notizen, Vol. xvi. No. 335.) found them in several plants, and thereupon has woven a prolix *soi-disant* theory *à la mode Française*, which, to a physiologist with more precise notions, carries its own refutation with it.

107 Upper part of a hair of *Borago officinalis*, at first thickened by a laminated deposit, and afterwards gradually filled up from above downwards by a solid material.




§ 64. The cells of the root sheath contain only air, and probably serve for the condensation of the aqueous vapour, and the conveying of it to the parenchyma of the root.

Here we have again an unsolved mystery of which I can give no other explanation, although the consideration of the conditions under which these roots occur in plants, growing for the most part without earth in an atmosphere saturated with moisture, may throw some light upon the subject. I do not allow much importance to the supposed great hygroscopicity of the spiral fibres, which is always put prominently forward by Meyen; but attribute more to the extreme porosity of this layer, which probably acts in the same way as freshly burned charcoal.

[108] Perpendicular section through the epidermis (*d*) of the leaf of *Ficus Carica*, by which two hairs (*a* and *b*), with dilated basal portion, are laid open. In the figure, the point of *b* is left. Both hairs are filled towards the upper part by gradual deposits, and these concretions (*c*) hang down into the basal dilatation of the hair-cell. In the hair marked *b*, this concretion consists of three united portions.

[109] Section perpendicular to the surface of the leaf of *Humulus Lupulus*, through the epidermis (*b*), and some of the subjacent parenchymatous cells. *a*, An epidermis-cell dilated inwardly into a vesicle, analogous to the hairs of *Ficus*. The narrower extremity is filled up, and from this part depends by a sort of peduncle a concretionary mass into the dilated portion of the cell.

# THIRD BOOK.

## MORPHOLOGY.

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§ 65. MORPHOLOGY is the study of the forms of plants, and of their several parts. It is divisible into a *general branch*, which elucidates all that has reference to plants and their organs in general; and a *special branch*, which treats of plants according to their principal groups, as well as their individual organs: and this latter branch, again, is separable into two parallel sections, namely, the delineation of external form, and the delineation of internal structure, or of the peculiar composition of plants and their parts from various tissues.

In my methodological introduction I have endeavoured to show that the external morphology of plants is really the most important section of Botany. A mere glance at the history of the science will convince any one of the truth of this view, for it is truly wonderful to observe how far it has succeeded, to the almost entire neglect of all other scientific knowledge, in taking possession of the material by merely examining its exterior, and arranging it in such a manner that the systems which, in recent times, have taken another path—I allude to the anatomico-physiological—have scarcely effected more than the introduction of extremely trifling changes, in some instances clearly untenable, and others at best of very doubtful validity. The morphological method of observation has certainly, from the origin of the science, been the basis of all treatises on Botany; but those who have thus pursued it have been far from taking a strictly scientific view of the question, or seeking in this way for the solution of its difficulties. This task is two-fold, at once empirical and theoretical. In its first character, the study requires us to examine into and characterise the fundamental forms which, as types, or conceptions of generic and specific shapes, constitute the basis of individual forms. In its second character, this study has to unfold the natural laws according to which these types are formed, and which control and explain the deviations that occur in individual forms from their prototypes. For the first, or empirical part of our researches, we may congratulate ourselves on having some little information, although of a very fragmentary nature; but in the second, or theoretical department, we have scarcely even an indication to guide us. That the solution of the difficulties must be sought by beginning from the simplest case is evident, and here Schwann has certainly shown eminent acuteness in establishing the analogy between the formation of crystals and that of cells; but unfortunately we have not yet brought the law of crystalline formation into the dominion of science. Thus at the present time we can do no more than specify the problem presented to Botany, the solution of which

is alone to be expected when the mathematical construction of the formation of crystals lies perfectly complete before us. If, however, this is ever to be effected, we must enter upon all possible construction in a very different way from what has hitherto been done. For this purpose, we must consider somewhat more exactly the characteristics of organic form, especially the vegetable, as opposed to the inorganic. The inorganic form, the crystal, is permanent when once formed; it is unchangeable; the individual (the individual existence) is the form itself, and by its solution and change of form a new individual arises. In the plant, on the other hand, the form is not stable, or permanent, but an ever-changing one. The analogies between the two hold good only in the simplest cases. The nucleus of a crystal originates in a definite form, and then passes through a series of forms, until it reaches the deduced crystalline form. As such it then remains unchangeable until the individual is destroyed with the form. Thus, certainly, it has a very simple history of development, but this continues merely so long as something is still being added to that which is already present—until the whole is completed. The cell is formed in a manner somewhat analogous to this, originating in a definite form, and passing through a series of changes, which, as it appears, only contribute new matter until the form is complete; this then remains stationary until its solution and the consequent destruction of its individuality. It is, however, wholly different in combined forms, and these it is which, with few exceptions, compose what we term plants. Here a number of cells combine together within definite external limits; but these cells themselves do not enter into the form as dead particles of the mass; they continue to develop new cells, whilst the old ones are partially destroyed: the newly originated cells change, by their arrangement, the form of the whole, and, since formation of new parts and destruction of the old are continually going on, the general boundary of the whole never appears as anything definitely fixed. As, however, this metamorphosis is constant in its nature, and only occurs in individual parts, we cannot regard each one of the forms resulting from this process as a new one, but merely as a slight modification of the one immediately preceding it; and this peculiar connection brings the whole to us as *one individual*, which, at its first appearance, may be entirely different in all its parts, both in shape and material, from what it is at last; but in the conception of which we must comprehend the whole series of changing forms, wherein the widely distant members have perhaps no element identical, if we would attain to scientific knowledge, if we would understand the object, and not merely acquire a disjointed, uncomprehended, and incomprehensible impression. From these considerations it follows, granting the paramount importance of the morphological method of observation, that we gain nothing by the comprehension of the forms complete at any one moment, but that we must trace out the law of morphological development, and direct our scientific inquiries, not to an individual complete at any one period, but to the comprehension of the collective constant series of normally changing forms. The conception of genera and species in Botany is consequently, therefore, not merely the result of a comparison, but also of a connection of the various individual characteristics with each other. In this manner we should lay a firm foundation for the inductions to lead us to a theory of organic morphology, if we could but succeed in completing the theory of the formation of inorganic forms. As yet we are far from this point, and simply because it is only in the

most recent times, and yet very imperfectly, that the importance of the study of the history of development has been acknowledged; although, without this, Botany would be wholly divested of all scientific principle. This deficiency renders it impossible as yet to treat morphology with scientific logical development, or in accordance with a perfectly systematic mode of arrangement, as will but too obviously appear in my manner of treating this subject, although the blame of this is only partially to be imputed to me. It seems, however, practicable perfectly to state the *problem*, and to this end I subjoin the following remarks.

We have to construct the laws of morphological formation, and to delineate the forms themselves. The first remains for the present a mere problem, the solution of which must be reserved for succeeding times. The second may be accomplished, although imperfectly. I say imperfectly, because, instead of those complete series of development of which we ought alone to treat, we only know a few individual conditions; and, therefore, the greatest portion of the task still lies unperformed before us. Here we must again distinguish between—1. Series of forms which occur in all or in very many plants of a very different nature, and may, therefore, especially serve as the foundation of the study of vegetable forms; that is, "general morphology." 2. Series of forms which are only peculiar to definite groups of plants: "special or comparative morphology." These two would further branch off into the consideration of form without reference to its composition from the different forms of the elementary organs, "external morphology;" and into the consideration of the manner in which forms are composed from individual tissues, "internal morphology" (the theory of structure — "comparative anatomy"). This last part falls, however, away from general morphology; for all that we can, for the present at least, say is, that every plant is composed of the different forms of the elementary organs which have already been treated of. Even with respect to the second part, in regard to comparative morphology, it appears to me unadvisable to divide the two sections, on account of our deficiency of material; I shall, therefore, in the examination of the individual groups and parts of plants, subjoin all that is known concerning their structure.

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# CHAPTER I.

## GENERAL MORPHOLOGY.

§ 66. The forms of individuals and their parts are the special objects to be considered by Morphology.

I. In scientific Botany we have to consider the separate cells, and, according to the empirical conception, plants, as individual organisms. In the latter relation we find individuals of different orders. The elementary organs combine to constitute definite forms (a simple plant, *planta simplex*). New and like individuals (buds, *gemmæ*) are formed by development upon the plant, and

frequently remain in connection with the parent plant, offering for our consideration one collective individual (a compound plant, *planta composita*). If only organs of propagation, or blossoms, proceed from the buds, we still term the plant simple. This composition is repeated in innumerable gradations.

Much has been written and disputed concerning the conception of the individual, without, however, elucidating the subject, principally owing to the misconception that still exists as to the origin of the conception. Now the individual is no conception, but the mere subjective comprehension of an actual object, presented to us under some given specific conception, and on this latter it alone depends whether the object is or is not an individual. Under the specific conception of the solar system, ours is an individual: in relation to the specific conception of a planetary body, it is an aggregate of many individuals. There is, therefore, no sense in contending as to whether a certain object is or is not an individual in the vegetable world, until the conception of the species, the plant, be perfectly defined. Now I have already shown in the introduction that we have hitherto been unable to comprehend plants collectively, with any degree of scientific perspicuity in a definite conception, but have merely given them in rough outline. The manner in which we take up the materials we have become acquainted with, and apply them as temporary scientific aids in defining the conceptions of the species of plants, is purely arbitrary, and can at most only give rise to a contest upon the applicability of this or that definition. I think, however, that, looking at the indubitable facts already mentioned, and the relations treated of in the course of these considerations, it will appear most advantageous and most useful, in a scientific point of view, to consider the vegetable cell as the general type of the plant (simple plant of the first order). Under this conception, *Protococcus* and other plants consisting of only one cell, and the spore and pollen-granule, will appear as individuals. Such individuals may, however, again, with a partial renunciation of their individual independence, combine under definite laws into definite forms (somewhat as the individual animals do in the globe of the *Volvox globator*). These again appear empirically as individual beings, under a conception of a species (simple plants of the second order) derived from the form of the normal connection of the elementary individuals. But we cannot stop here, since Nature herself combines these individuals, under a definite form*, into larger associations, whence we draw the third conception of the plant, from a connection, as it were, of the second power (compound plants — plants of the third order). The simple plant proceeding from the combination of the elementary individuals is then termed a bud (*gemma*), in the composition of plants of the third order. This last conception, however, admits only of strict application where the form of the connection of the elementary individuals is quite regularly defined ; and this we first meet with from Mosses upward ; the connection being so loose in the *Algæ*, Lichens, and *Fungi*, that we cannot well distinguish between an individual development of the plant, and a repeated composition of the same ; or, in other words, between growth and the formation of buds (gemmation). We regard them provisionally as simple plants (of the second order).

* "Gemmæ totidem herbæ," Linné. Phil. Bot. § 132. We find this relation already correctly conceived here.

As, however, the formation of reproductive organs, or blossoms, in every case completely hinders the further development of the simple plant in the same direction, we still apply this term of simple plants to those in which the buds are solely reproductive organs, or blossoms, and which, consequently, are individuals incapable of growth.

§ 67. II. Under the parts of the plants whose forms have to be considered, I understand the constant subdivisions of the total form which present themselves as subjectively perceptible within the sphere of a group of plants, and these parts I name the organs of plants.

Among the deplorable confusions which a false analogy with animals has introduced into Botany, we must reckon the attempt that is commonly made to define the organs of plants by their physiological characteristics, with a thorough disregard of the fact that we know of no organ in which the individual cells have not a perfectly independent life, only *occasionally* so far modified as to cause one definite phenomenon of this life to appear especially prominent (as we shall subsequently show under the head of Organology), without the others becoming, on that account, completely suppressed. Through what vital part can the plant not imbibe nutriment, form secretions, and develop itself? If even these most important functions are not apportioned to a definite organ, how can we still universally talk of the physiological differences of organs? It appears to me that everything regarding this subject has to be based upon morphology. It must be left to Special Morphology to determine whether, and what, organs are thus formed; while it belongs to Organology to discover how far, in these organs, particular definite phenomena of cell-life are developed for the production of one remarkable collective effect.

§ 68. The condition of all morphological development is extension in space. Every plant, every part of a plant, may therefore appear in the form of a *line* — *Conferva, Usnea, Cuscuta,* most stems, the leaves of *Juncus, Triglochin,* &c.; in the form of a *surface,* as *Ulva, Parmelia, Lacis, Marathrum,* the stem of *Opuntia, Phyllanthus, Ruscus,* ordinary leaves, &c., or be expanded into a *solid,* as *Protococcus, Undina, Mammillaria, Melocactus,* and the leaves of the species of *Sedum,* or *Mesembryanthemum.*

The mere prevalence of one dimension must never be received as a characteristic in our conception of a group of plants, or of a part of a plant, since herein experience leads to no definite laws; *à priori,* however, expansions in all three dimensions of space are equally possible. It is certainly very important to hold firmly the general validity of this proposition, for, simple as it is, it has frequently been contested, in deciding upon the nature of individual organs according to mere relations of dimension.

§ 69. Linear structures (fig. 110.) are still more exactly defined according to a sectional figure, as *teres* (*a*), *anceps* (*b*), *triqueter* (*c*),

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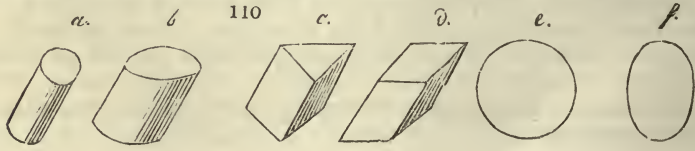
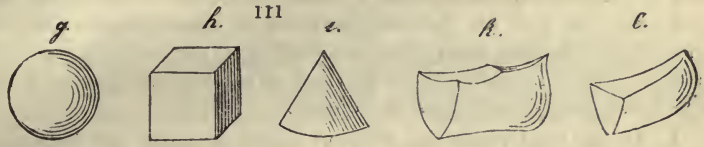


*quandrangularis* (*d*), &c. The forms of surfaces are never enclosed by exactly straight lines, but are mostly bounded by curves, and, in accordance with these, are either *rotundus* (*e*), *ovatus* (*f*), &c. Lastly, the forms of solids are designated according to their resem-




blance to stereometric figures (fig. 111.), as *globularis* (*g*), *cubicus* (*h*), *conicus* (*i*), &c.; or according to incidental resemblances to known objects, as *acinaciforme* (*k*), *dolabriforme* (*l*), *mammillaris*, &c.

It cannot be my object to give here the whole of this terminology, which is in part so very superfluously diffuse, and yet in many respects most inappropriate. I would merely indicate the method in which these expressions have been sought for, and the point of view from which they must be explained. No one can deny that it is absolutely disgusting to read in botanical works, for instance, that a leaf may be flat and oval, or lanceolate or linear, and likewise thick and fleshy; and then again with reference to the stem, that it may also be thick and fleshy, or flat and oval, or lanceolate, or linear; and, finally, the same rigmarole repeated about the petals, anthers, and a hundred other parts, by which the time of the scholar is most lamentably wasted. These general adjective technical expressions are not peculiar to Botany, but belong to the natural sciences in general; they properly constitute a special study, the scientific theory of observation, which Illiger* made an attempt, although an unsuccessful one, to systematise. Since then the subject has remained untouched. The more recent theories of the schools have, however, seriously endeavoured to educate boys gradually into sensible beings, with open eyes and senses; whilst philology seemed in former days to have trained men to little better than mere book-worms, and spoiled them for all sound and clear comprehension by observation; whence have come into our science so many useless wildernesses of words, and so little simplicity and correctness of observation. By way of reference for all these useless, and in some degree foolish, designations, I would recommend Bischoff's † little hand-book of botanical technical terms, as the simplest and most concise. I shall here, and in my subsequent descriptions, only indicate the correct arrangement of the technical terms according to the roots of their meanings, and limit myself as much as possible to the use of such as designate something peculiarly botanical. I would here remark, however, that we soon find our stock of accurately-defining mathematical expressions exhausted, and that we have then no alternative left but to use figurative terms; and here the fate of the art of scientific description depends upon the greater or lesser skill of the individual. The main cause of the great deficiency that characterises our terminology for the natural sciences, has arisen from heedlessness in

* J. K. W. Illiger's Versuch einer systematischen, vollständigen Terminologie für das Thier- und Pflanzenreich. Helmstadt, 1808.

† Bischoff, Lehrbuch der Botanik. Appendix. Stuttgart, 1839.

the choice of words, it having appeared sufficient in most instances that these terms applied to the case immediately in point, whilst an incidental accessory signification of the word often rendered it wholly inapplicable in its general interpretation.

§ 70. As the comparison with geometrical figures cannot be carried out very far, and as the designations of resemblance with other known objects may easily become too vague and uncertain, we must have recourse to some artifices to aid us in the description of forms. They are partly described as follows:—

I. In the first place the general outlines must be defined, and this is done by supposing all the external points in a superficies to be united by a line, and those of a corporeal form by a surface, and then applying some term to this line or surface. We thus obtain the following designations (fig. 112.): —

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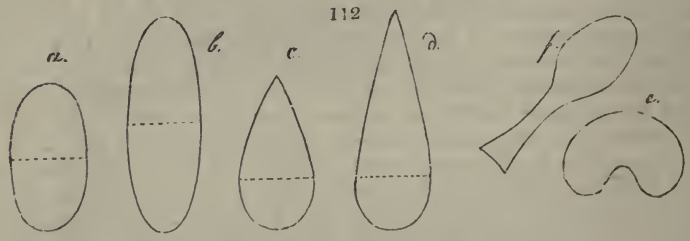


*A.* The greatest transversal diameter in the centre.

1. About twice as long as it is broad, oval (*a*).

2. Three or more times as long as it is broad, oblong (*b*).

*B.* The greatest transversal diameter in the lower third.

1. Twice as long as it is broad, ovate (*c*), or if the greatest diameter lie in the upper third it is conversely ovate (*obovatus*).

2. Three and more times longer than it is broad, lance-shaped (*lanceolatus*) (*d*).

*C.* Broader than it is long; rounded off at the one extremity, and excavated at the other, kidney-shaped (*reniformis*) (*e*).

*D.* The upper part broader than the lower, which ends in a decidedly narrower portion: in bodies this form is club-shaped (*clavatus*); in surfaces it is spatula-shaped (*spathulatus*) (*f*).

II. The main division of these forms is further given according to the following gradations: for instance, we draw the divisions upon an imaginary medial line, or around a central point (fig. 113.), and divide the distance between this line or point to the circumference into two parts.

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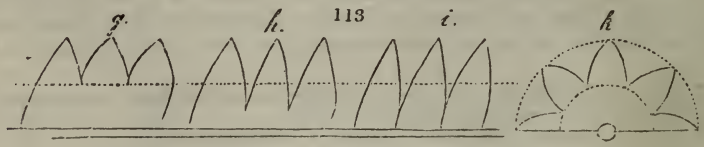
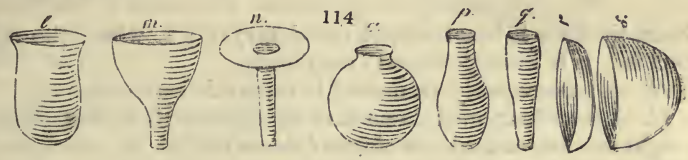


*A.* Divided to about half-way, cleft (*fissus*) (*g*, *h*); the individual parts are lobes (*lobi*).

*B.* Divided beyond the middle, divided (*partitus*) (*h*); the individual portions, parts (*partes*).

*C.* Divided to the assumed line or point, cut up (*sectus*) (*i*); and the individual portions, segments (*segmenta*).

III. We have a series of tolerably definite expressions for the outlines of hollow forms, in which we make no special reference to the division. The expressions are comparisons, and explain themselves (fig. 114.).




Bell-shaped (*campanulatus*) (*l*), funnel-shaped (*infundibuliformis*) (*m*), salver-shaped (*hypocrateriformis*)* (*n*), pitcher-shaped (*urceolatus*) (*o*), flask-shaped (*lagenæformis*) (*p*), tube-shaped (*tubuliformis*) (*q*), cup-shaped (*cupuliformis*) (*s*), plate-shaped (*patellæformis*) (*r*). In all these forms where the distinction is applicable, the lower and more cylindrical part is termed the tube (*tubus*), and the upper and more expanded the limb (*limbus*), and the point of junction the throat (*faux*).

§ 71. In the further description of forms we especially examine the base and the apex. The region of a form by which it is attached, as, for instance, a leaf on a stalk, is termed the base (*basis*), and the opposite free end the point or summit (*apex*). There are special designations for both (fig. 115.).

I. *A.* Apex with a notch, where this is 1. acute, excised (*excisus*) (*a*); 2. where the angle is rounded off, it is emarginate (*emarginatus*) (*b*).

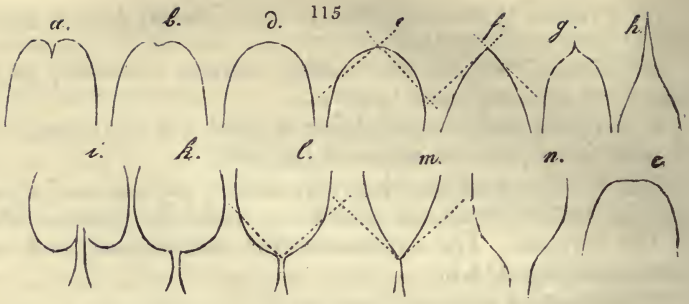
*B.* Where the apex is abrupt, either truncate (*truncatus*) (*c*), or when rounded off, rounded (*rotundatus*) (*d*).

*C.* Where the apex terminates in an angle with convex sides, 1. in a right or larger angle, the form is obtuse (*obtusus*) (*e*); 2. less than a right angle it is acute (*acutus*) (*f*).

*D.* Where the apex terminating in an angle with concave sides is 1. suddenly and sharply acute, the form is mucronate (*mucronatus*) (*g*); 2. gradually and long pointed it is peaked (*acuminatus*) (*h*).

II. *A.* A base with a penetrating angle: 1. where the angle is

* This expression will be best understood by those who are familiar with the form of the plate or salver on which glasses were placed in the middle ages, as we find it in old collections, or delineated by the old masters.



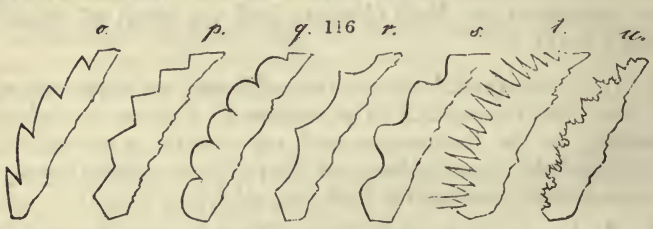

acute, the form is heart-shaped (*cordatus*) (*i*); 2. where the angle is rounded, it is kidney-shaped (*reniformis*).

*B.* A base roundly truncated is rounded (*rotundata*) (*k*).

*C.* A base continued down into an angle with convex sides, 1. in a right and larger angle, is obtuse (*obtusa*) (*l*); 2. in less than a right angle, is acute (*acuta*) (*m*).

*D.* A base terminating in an angle with concave sides is attenuated (*attenuata*) (*n*).

All these expressions apply equally to solid and to superficial forms; but as the latter only can have a margin (*margo*), the following terms are applicable to them alone, being derived from slighter marginal irregularities of figure (fig. 116.).




*A.* With acute angles, either projecting or penetrating: 1. where the sides are unequal, the margins are said to be serrate (*serratus*) (*o*); 2. the sides equal, toothed (*dentatus*) (*p*). The separate projections in either case are termed teeth (*dentes*).

*B.* Where the projecting points are rounded, and the penetrating angle acute, the outline is notched (*crenatus*) (*q*), and the separate projections are crenatures (*crenaturæ*).

*C.* Where the projecting angle is acute, and the penetrating one rounded, the outline is scooped out (*repandus*), and the separate projections are teeth (*dentes*).

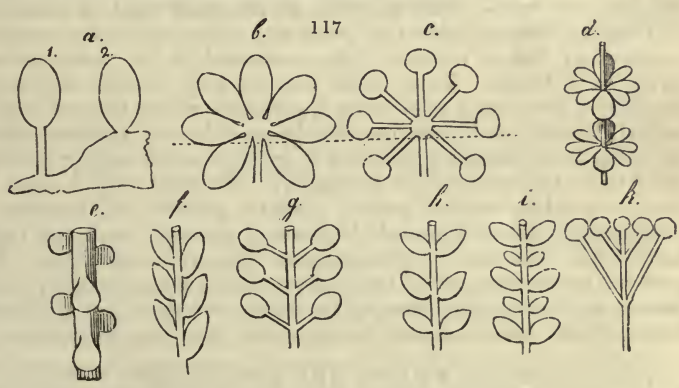
*D.* Where the projecting and penetrating angles are rounded, the margin is sinuate (*sinuatus*) (*s*), and the separate parts are termed lobes (*lobuli*).

*E.* Where the projecting and penetrating angles are very acute, and the sections very narrow and long, the outline is ciliate (*ciliatus*) (*t*), and the separate parts are termed cilia (*ciliæ*).

*F.* Where the projecting and the penetrating angle and the lobes are very irregular, and small and close, the margins are said to be bitten out (*erosus*) (*u*).

§ 72. The simple fundamental forms may combine again by uniting together according to the three dimensions of space, whence an endless variety of compound structures is produced, for a very few of which only we have designations which give clear impressions, as, for instance, spherical forms connected in a linear series are termed (*moniliformes*) necklace-shaped or beaded. A spherical or flat part, the base of which is connected by a linear part (*stipes*) with another, is said to be stalked (*pars stipitata*) (fig. 117. *a*, 1.); if it be immediately connected with some other part, it is sessile (*sessilis*) (*a*, 2.).

The most important relations have been comprised under the following method of consideration: — A simple form is regarded as the main part, the supporter of the others, the axis on which they are attached as limbs or accessories of the whole (*articuli, partes appendiculares vel laterales*). In the first place, a distinction is made according to the form of the axis, whether it be elongated or not; and next, according to the form of the lateral parts, whether they are stalked; further, according to the arrangement of the lateral parts on the axis; and, finally, according to their different relative size. We thus obtain the following distinctions: —




*A.* The axis spherical or short.

A. When all the lateral parts lie on one plane (*b, c*), they are hand- or finger-shaped (*partes palmatæ, digitatæ*).

B. When they surround the axis on all sides:

1. Sessile lateral parts are in heads (*p. capitatæ*) (*b*); *
2. Stalked lateral parts are in umbels (*p. umbellatæ*) (*c*).

*B.* The axis elongated.

A. Lateral parts of equal length, from below upward.

* Or at the end of an elongated axis, also tufted (*p. comosæ*).

1. When pointing in all directions.

*a.* Many arising nearly at one point.

*α.* Repeated at intervals along the axis, whorled (*p. verticillatæ*) (*d*).

*β.* On the base of the axis, rosette-shaped parts (*p. rosulatæ*).

*b.* Arising at different heights, scattered, spirally arranged parts (*p. sparsæ, spiraliter positæ*) (*e*).

*α.* Sessile lateral parts, spiked (*p. spicatæ*) (*f*).

*β.* Stalked lateral parts, clustered or racemose (*p. racemosæ*) (*g*).

2. When lying in one plane.

*a.* Only on one side of the axis, unilateral or secund (*p. secundæ*).

*b.* On both sides of the axis.

*α.* All equally long, pinnate (*p. pinnatæ*) (*h*).

*β.* Alternately long and short, interruptedly pinnate (*p. interrupte pinnatæ*) (*i*).

B. Where the lateral parts decrease gradually in length from below upward, so that the points lie in one plane, pyramidal parts, corymbs (*p. fastigiatæ, corymbi*) (*k*).*

Here, as we have already remarked, perfect completeness is not aimed at; nor, indeed, is it attainable. As in every other instance, our terminology is here an unscientific chaos. Expressions have been constantly adopted for mere individual cases; and as observation becomes more extended, the expressions admit either but imperfectly or not at all of being further applied to the general characteristics which the individual cases present, while these, after all, are precisely what we want to name. But we can scarcely expect to attain to a strictly scientific morphological terminology before we have fully succeeded in the mathematical construction of forms. In the mean time we may, in some degree, prepare for this by abstaining from using expressions which indicate nothing peculiarly relating to plants, but merely conditions of simple combinations of forms, in accidental application to wholly special cases, without, at the same time, explaining their generality. We might, with equal correctness, talk of head-shaped, united, pinnate, palmate, &c., crystals. What distinguishes ears and heads in blossoms is precisely similar to that which marks the difference of *folia sparsa* from *foliis rosulatis.* We comprehend under these terms nothing peculiarly characteristic of blossoms, leaves, or, indeed, any part of the plant, but merely a combination of forms, wholly independent of the nature of the forms themselves.

§ 73. As soon as we meet with more intricate combinations, or less definite forms, nothing remains for us but to combine these expressions, or choose wholly indefinite comparisons; thus we say *palmatifid* parts (*p. palmatifidæ*), *bipinnate* parts (*p. bipinnatæ*), &c.; or we designate forms as helmets, hoods, spurs, &c., which are almost all expressions which are intelligible merely within a definite sphere of forms, and consequently relate only to special botany.

Finally, to express small inequalities on the surface, a large number of terms have been made use of, which in like manner are for the most part figurative, and admit of no scientific strictness of

* Several corymbs combined form a cyme (*cyma*).

applications: as, for instance, *aciculatus*, as if torn by a needle; *rimosus*, with fissures or chinks; *sulcatus*, *punctatus*, *scrobiculatus*, *granulosus*, *verrucosus*, &c.; and to these we may add the designations in use for a hairy surface, as, for instance, *arachnoideus*, *lanuginosus*, *tomentosus*, *pubescens*, *pilosus*, *setosus*, *strigosus*, &c. Scientific exactness can only be attained here by a more accurate description of the parts in question, and especially by the characterisation of their morphological or anatomical signification.

§ 74. In all plants, with the exception of the few which consist only of one cell, the form depends upon the manner in which the cells are combined together. The development of forms is here dependent on two essential points, namely, the arrangement of the newly formed cells, and the different expansion of those already existing. These two determining causes are normally definite for every individual species of plant and for each separate organ, but are entirely incidental for plants in general. The expansion of a plant, or the part of a plant, in one, two, or three dimensions of space, may depend as well upon the arrangement of the developing cells as upon the expansion of those already developed, or as upon the two causes combined.

This subject has hitherto been wholly neglected, although it must form the foundation of the whole science of morphology, since on this alone depends the development of forms in plants. The whole question will be understood in all its relations if we only remember that when four new cells arise in one cell (fig. 118.), they may be within the parent-cell, either

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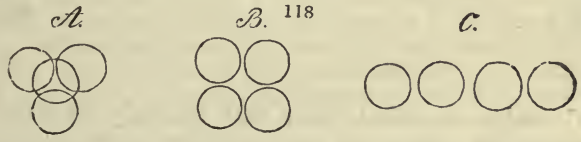
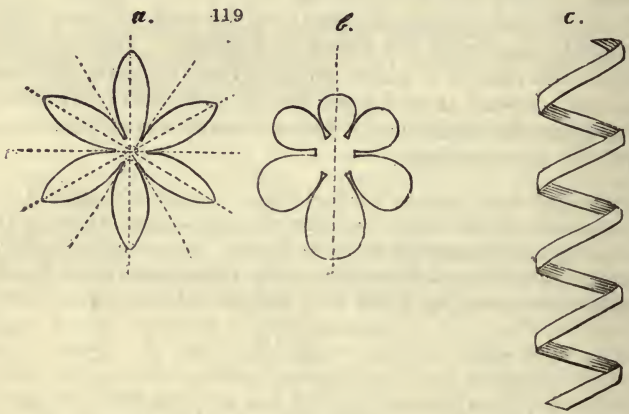



in a row, linearly (*C*), or two and two beside each other (*B*), forming a plane, or, finally, may lie within the parent-cell, like the corners of the tetraedron (*A*), forming a solid body. Owing to the great difficulty, in most cases, of observing the first origin of cells, a long time must elapse before we shall be able to account for the origin of different forms. All future investigations into the history of development must, however, necessarily be directed to this essential point, and it is here, therefore, that we have to expect the most interesting laws for the science of morphology. We are unable, at present, to express any general statements, and it must, therefore, suffice here to have drawn attention to the paramount importance of this point. A few more special amplifications will be met with in a subsequent part of our work, especially with reference to the stem and the foliar organs. As the foundation of every plant is in all cases one individual cell (spore or embryonary vesicle), within or out of which the new cells which gradually form the whole plant are developed, in each primary cell must lie the conditions according to which the subsequently developed cells are arranged: since, however, the expansion of the individual cell in the three dimensions of space depends essentially upon

the nutrition of its membrane, and the latter upon the presence of a nutrient fluid, that second cause of form will almost always be a consequence of the first, so soon as the cells are removed from an immediate contact with the nutrient fluid. A linear arrangement of the cells may, therefore, easily produce a greater expansion lengthwise, &c. By way of illustration of the regular arrangement of newly developed cells, I will only cite the case of two cells of the stomate. Here two young cells arise in a parent-cell, formed, without exception, exactly in such a manner that they lie in a plane with the epidermis, and never so as to lie one upon another, as seen from the exterior of this membrane.

§ 75. Regular mathematical forms never occur in plants, with the exception of the spherical form of individual cells. We term those forms in plants *regular* which admit of being divided into two equal parts by many sections passing through an imaginary




axis (*a*); and *symmetrical*, those that can only be divided by *one single section* into two equal parts, standing in the relation of right and left to each other (*b*).

As each separate cell is a wholly independent individual, and as only a few simple individuals of the second order are formed by the mere collection of cells, while most plants acquire their whole form from the combination of these latter; and since each individual of the first and second order may be considered *per se*, owing to the independence of external influences possessed by its existence, without, at the same time, its being on that account exempt from a connection with the whole, it will easily be understood how very indefinite the form of most plants must be. We consequently meet with *regularity*, or even *symmetry*, in the sense above applied to the terms, in but a very small number of *entire* plants, as, for instance, in *Protococcus*, *Phascum*, *Equisetum*, *Wolffia*, *Melocactus*. We more frequently meet with both in the individual parts of plants, especially in the reproductive apparatus of the higher plants which have the closest morphological and physiological connection; for instance, in the capsule of mosses, in blossoms and fruits; we also often find only symmetry, at least in the leaves, and in whole individuals of the

second order, as in young shoots. Hugo Mohl * has collected many interesting facts with reference to this, but as yet we have not been able to deduce any results from them.

§ 76. A form that frequently occurs in the plant, and which appears to be especially characteristic, is the *spiral*, most constantly and normally appearing as a thickening layer, in the vital processes of the individual cell (see above, § 18.); also in the arrangement of the chlorophyll in *Spirogyra*, *Chara*; again in the spiral position of the nodose thickening of the cell-wall (see § 17.), in the very frequently evident spiral arrangement of appendicular parts round an axis; and, finally, in the spiral twistings of elongated parts, as tendrils and twining plants.

The facts adduced in the above paragraph are indisputable, and decidedly indicate a certain connection between a spiral direction and some peculiarity inherent in the nature of plants; but we must beware of overrating the importance of these facts, since they present much that is but vague and uncertain. In tendrils and twining plants, the phenomenon admits of a different explanation, for every filiform part, when wound round a stick, must form a spiral, which no one would seek to explain from the nature of an iron wire or a hemp cord. With respect to the spiral position of appendicular organs, appearance, or even strict mathematical measurement, may in many cases confirm the view of the existence of this peculiarity, as, for instance, in the cones of *Coniferæ*, in the warts of *Mammillariæ*, and in the fruits of the sun-flower; but it cannot be denied, at the same time, that in most of these cases the leaves decidedly do not form any mathematical spiral, and that it can only be proved that the law discovered for the spiral may be tolerably well applied to the arrangement of leaves, when only we bring the leaves a little into order. It seems to be entirely forgotten here, that all the points scattered upon a cylinder (and a stem is seldom or never a mathematical cylinder) may be united by a spiral, if we consider the distances of all the points from the base as fractional parts of the length of the cylinder, and assume that the common measure of these fractional parts is the distance between every two windings of the spiral. We ought, however, only to assume that there is the spiral indicated in the arrangement of the points when the distance between the two points is everywhere equal. But this requirement is only to be fulfilled by an arbitrary pushing aside of the points (the places at which the leaves are inserted), or by the assumption of an abortion, which we cannot find in nature. This view will acquire a true significance in the observation of the vegetable organism when we are able to show from what property of the plant a spiral arrangement must necessarily result, and the laws on which the individual irregularities depend. The two opposite views of Schimper and the brothers Bravais plainly demonstrate how arbitrary every thing is that has reference to the subject. I shall have occasion to revert to this when I come to speak of the leaves of the *Phanerogamia*. The spiral arrangement of the thickening layer in the cell seems evidently the most certain, but even in this we have the mere naked fact, and not a single idea how it may be methodically derived from the nature of the cell of the plant. It is manifest that the comparisons

* Hugo Mohl, Ueber die Symmetrie der Pflanzen. Tübingen, 1838.

made with a magneto-electric spiral* are a mere jest, and a very superficial one, since we have not as yet obtained any proof, based upon the most remote appearance of probability, of the presence of a galvanic current, for which there is not even a semblance of possibility when we consider the damp, and consequently universally conducting, condition of the cell-membranes.

§ 77. We have, as yet, no general numerical laws for plants. Indications of such admit, perhaps, of being traced from the fact that, in the far greater majority of cases, two, four, or eight young cells are formed within the parent-cell, as in *Tetraspora*, in the spores of the *Octosporidia*, Mosses, and the pollen of *Phanerogamia*. To these we may probably also add the frequently regular occurrence of definite numbers in whorls, as the recurrence of the number three in the parts of the flower of the monocotyledons, and the number five in the dicotyledons.

All these specified relations have already often been used in mere childish numerical jugglery; individual cases having been arbitrarily selected to confirm a preconceived theory, the exceptions being disregarded, fashioned by means of just as arbitrarily imagined fictions into a form adapted to the pretended theory. We cannot as yet decide, even with the most remote approximation to probability, if, for instance, the three petals of a monocotyledonous plant are to be regarded as a triple whorl or as a three-limbed spiral. These two must, however, be very differently derived from the nature of the plant, and, in the latter view, the contest originating in the hitherto equally balanced hypotheses of Schimper and Bravais would still remain to be decided. Before we can give any probability to such a deduction drawn from the nature of the vegetable organism, it is at any rate but just, amid the large number of exceptions present before us, to consider the more frequent occurrence of one or other number as purely accidental to plants in general. This occurrence of the numbers 2, 4, 8 in the young cells seems to possess more the appearance of systematic arrangement, but here we are utterly unable to discover any connection with the nature of the vegetable cell. We shall probably have to wait long before we meet with even indications more definite.

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## CHAPTER II.

### SPECIAL MORPHOLOGY.

§ 78. The history of development forms the groundwork for all special botanical morphology, and we must, therefore, have reference to it in choosing our general modes of classification. Every plant originates from a cell; and the first difference among

* As, for instance, in Link's Element. Phil. Bot. ed. 2. t. i. p. 177.

cells capable of affecting the form of their development is, whether these cells become at an early period, isolated and independent, whether they remain for a longer period of time, till their subsequent development, merely as parts of the parent organism, as secondary cells within the parent cell. In the latter case the propagating cells are enclosed within a parent cell (*sporangium*), while in the former they are contained *free* in a cavity of certain portions of cellular tissue (*sporocarp, anther cell*); and, grounding my division on these points, I divide plants into covered-spored (*Angiosporæ*) and naked-spored (*Gymnosporæ*).

The next difference to be considered affects the manner in which the spores are developed, whether under the influence of other cells of the parent plant or not. We find that this affords us another ground of division for the *Gymnosporæ*, for the propagating cell either develops itself freely to a new *asexual* plant (*Plantæ agamicæ*), which, together with the *Angiosporæ*, have been termed, since the time of Linnæus, *Cryptogamæ;* or it requires for its development to be previously encased by, and brought under the material influence of, certain cells of the parent plant (sexual plants (*Pl. gamicæ*). Finally, under this last head, we may admit another difference between *plants having no definite point of union for the sexes* (*Pl. athalamicæ*), where the two different kinds of cells, or cellular masses, only combine subsequently to their separation from the parent plant, and *plants having a definite point of union for the sexes* (*Pl. thalamicæ* or *Phanerogamæ*), where the propagating cell is taken up at a definite part of the parent plant, and there developed for a time previous to its separation from it.

My words would be most erroneously construed, were it supposed for a moment that I was arbitrarily constructing a form of division, and then arranging the plants in accordance with it. So far from this, it has been my endeavour first to form the groups by a comparison of the whole history of development, and then seek for a characteristic by which to designate the groups thus found. On taking a general survey of the whole vegetable kingdom, unbiassed by previously conceived views, we should be inevitably led to separate the *Algæ*, Lichens, and *Fungi* from all other plants, and arrange them in one common group, but it must be left to a subsequently acquired and a more extended knowledge of all plants to determine the strict confines and the combination of characteristics appertaining to this group. It cannot, however, be denied that an essential difference is manifested in the formative principles of the already named lower groups, and the higher plants, which, although apparent to every observer, science is not always able to characterise. Granting even that in the form of separate lateral parts, as, for instance, in the so-called fronds of the *Florideæ*, an analogy may really be found with the leaf-formation of higher plants, this would only be an evidence of the deficient condition of our knowledge, but could not efface the line of demarcation which has here evidently been drawn by Nature. Nägeli, in opposing my mode of division, has afforded a most signal proof of the difficulty, to those who have once been led astray in dogmatising, of extricating themselves, although with the best

will to do so, or even of comprehending the more correct views of others. Nägeli might have spared himself the trouble of contesting against my system, as I have expressly protested against any such misconception. No one possessed of a capacity for classification will ever concur in drawing a main line of demarcation between *Florideæ* and the other *Algæ* (as Nägeli does), so that the former are not made to find the *most proximate* affinity to the latter; and the mere subtilty of dogmatism selects a character, or a mode of division, and then separates the groups in accordance with it. According to my views, it would form a more natural classification if one were to insert the three lowest groups of plants as a special kingdom between the animal and the vegetable, rather than to divide a portion from this department and subjoin it to the higher orders of plants. No ground for such a division, no systematic principle, justifies us in adopting this mode of separation; simply the judgment from appearances, if I may so express myself, which requires that science should corroborate it; the expression of the same sound sense that has named the heads of the *Compositæ* a flower, and which, indeed, may demand the assistance of science, but may never be slighted by her. The task of science is to refine and cultivate the sense of perceptive comprehension, to render the appreciation of the true and natural more acutely sensitive, and, finally, to ground the dictum of the senses upon the scientific basis derived from the study of comparative development. As the principal groups are adopted especially from observation, their designations may naturally be derived from various characters, since it is only by degrees that we are enabled to substitute in the place of these the only correct ground of division — namely, that founded upon the history of development. This demand for uniformity of division carries us away from the purely inductive method, which, while it always follows a definite course, is conscious of being still far removed from the aim it strives to attain.

Notwithstanding Nägeli's opposition to them, my provisional designations of the two principal groups, as *Angiosporæ* and *Gymnosporæ*, seem to me perfectly applicable. This difference still remains, that in all *Angiosporæ* the propagating cells remain firmly enclosed in the parenchyma of the parent plant, forming one continuous tissue, until their separation from it, while in all other plants the propagating cells remain perfectly free, unconnected with the tissue of the parent plant, and merely enclosed within its cavities. As yet, we are deficient in the investigations necessary for substituting any term derived from the history of development in the place of this character. As far as I am able to judge, the following difference seems to be indicated: — In the *Angiosporæ* the *whole* propagating cell is converted into the new plant, and in the *Gymnosporæ* the propagating cell extends into a pouch-like cavity varying in length, one protruded cellular extremity only being developed into a new plant, while the other dies off. This characteristic is only lost, but its truth at the same time confirmed, in the Liverwort, which evidently forms the transition in the relation already designated. But *here* we are deficient in our knowledge of the more minute phenomena of development of the Lichens and the *Lycopodiaceæ*. The same difficulty meets us in the classification into asexual* and sexual plants.

* It will of course be understood that the word "sex" means nothing beyond a mere indication, it being at any rate at present incorrect to attach to the term the meaning current with respect to animal life. It would be highly desirable wholly to banish the use of this equivocal term, as many misconceptions might thus be avoided.

The law of development might perhaps aid us in finding the distinguishing differences in the development of the proembryo in the first named, since between the first development of the propagating cell and the actual development of the perfect plant a passing stage of transition is to be met with, which manifests a certain analogy with the formations of the groups of the *Angiosporæ*. The further subdivision of the sexual plants is, however, wholly based upon the law of development. The *Rhizocarpeæ*, as the *Athalamicæ*, constitute an admirable medial stage between the *Agamæ* and the *Phanerogamæ;* agreeing with the former in this, that the propagating cell is developed to a new plant, without any intermediate interruption*, and with the latter in their development not being free, but being effected at first in the interior of a cellular mass engendered by the parent plant.

There are other characteristics denoting the internal and external form of developed plants, which coincide in a remarkable manner with those above given, and derived from the law of development; these have been already partially, but very imperfectly, treated of. The *Angiosporæ* may also be termed cellular plants (*Pl. cellulares*), since they afford no indication of a current of sap passing through definitely arranged elongated cells (vascular bundles). In like manner, their external form may be defined as stemless (*Pl. acaules*, *Thallophytæ* Endl.), as we have not hitherto been able to detect any sharply defined morphological contrast between a lateral parenchymatic extension (leaves) and a body uniting these (stem). In contradistinction the *Angiosporæ* are designated as vascular plants (*Pl. vasculares*), and as plants having stems (*Pl. caulinæ*, *Cormophytæ* Endl.). The divisions of the *Gymnosporæ* would correspond to plants having simultaneous and progressive vascular bundles (§ 26.), and plants with or without an apparatus for propagation, and finally characteristics drawn from the nature of the vascular bundles and the morphology of the flowering portions of the plant might perhaps be added to the Athalamic and Thalamic orders, but unfortunately we are still deficient, especially with respect to the *Rhizocarpeæ*, in the more accurate investigations necessary to guide us. We cannot too frequently repeat, that all our subdivisions are, and must be, regarded as merely provisional, and as extremely deficient, as a correct classification can only be derived from a complete knowledge of the law of comparative development, from the attainment of which we are still infinitely far removed. All that we can say is, that all divisions grounded upon characteristics which appertain in their nature only to a definite stage of development, and do not stand in the most immediate connection with the developing process, must either be decidedly false, or, at best, simply accidental, and do not by their own value constitute the natural groups. On the other hand, every classification must remain permanent that has been derived from characteristics depending upon the law of development. Thus the line of demarcation which has been laid down between the *Cryptogamia* and the *Phanerogamia* will ever continue, even though these divisions may not always be regarded as those possessing the highest importance. The recent attempts to range the *Cycadaceæ* under the head of the Ferns rests on such erroneous conceptions of vegetable nature, and are based upon observations of so inessential a kind, that they cannot be long maintained. In the same way, Monocotyledons and Dicotyledons will always remain separated, and notwithstanding all the

* They do not pass through a stage of seminal maturity, or slumber in embryonic life.

substitutes that have been proposed, tried like some new article of fashion, and then rejected, as *Endogenes* and *Exogenes*, *Amphibryæ* and *Acramphibryæ*, *Loxinæ* and *Orthoinæ*, *Exorhizæ* and *Endorhizæ*, &c., we shall still have to return to the old division, as being the best and most applicable of all, because it rests upon what is most essential in the morphological law of development. It is only to be lamented that so much valuable time and such fine powers, which might be devoted to well-grounded observations on the law of development, and consequently to the special furtherance of science, should have been wasted in this utterly useless game of system-making.

I must, however, be permitted to remark, that, with very few exceptions, all our classifications of plants into individual larger or smaller groups are still so unstable, that we are obliged almost in every case to designate certain forms as mere transitions from one group to another. In order to avoid misconception on this head, we must, however, consider more attentively what is meant by the term *Transition*. We may interpret it in three different ways. In the first place, it may mean an individual transition of the nature that occurs when one and the same being passes through different phases of its existence at different times, and may therefore at various periods fall under various specific heads. We have already pointed out the absurdity of such an idea; it has nevertheless met with supporters among persons who have given evidence, by the maintenance of such views, of their own ignorance and thorough want of philosophical clearness of understanding. In the present highly deficient state of our knowledge regarding simple vegetable organisms, a transitional stage of development must often be mistaken, for a time, to be an independent species; but as soon as further observations have shown the course of its development to another species, the transiently established classification falls to the ground, and we are as little disposed to regard the plant as a separate species as we should be thus to designate the pollen-granule and the seed or the ovum in animals. The matter appears so simple, that we should be struck with astonishment that any one could even have arrived at the conclusions embraced by Agardh *, Hornschuch †, Meyen ‡, and others, but that we know that Schelling's so-called Philosophy of Nature has misled so many into the belief that there is something scientific in the subtleties of comparison and analogy. The proembryo of Mosses is as little a Conferva as the pollen-granule of the *Zostera marina*. Both are dependent structures, which only acquire their full signification in the complete connection of the law of development. Thus the whole of what Agardh and others have enlarged so much upon simply amounts to this, that Mosses as well as all other plants consist of differently formed cells at various periods of their existence.

The second interpretation that may be given to the expression *transition*, does designate actually different species, the characters of which are so similar in the two most immediately allied species, or approach so nearly through the individual variations, that it is impossible to lay hold of any one individual character which may separate the whole into two groups, although their extremes seem to indicate or demand some such division. Here we must in the first place remember

* Allgemeine Biologie der Pflanzen, from the Swedish by Creplin. Greifswald, 1832, § 42.

† Act. Acad. Leop. Car. x.

‡ Robert Brown's Miscellaneous Writings. [German edition, in 5 vols. For the purpose of illustration, it contains the papers and remarks of other botanists.—Trans.]

that Nature presents no system for our scientific considerations, but simply individual beings, between which no middle form can be imagined, since the character of individuality precludes the possibility of variations. It is we ourselves who introduce into the number of individual beings an arrangement and classification into larger or smaller groups, species, races, or families. On finding a greater degree of uniformity among a certain number of individuals, we arrange these together, and then proceed to seek for an expression by which to characterise this group. And it is only when we have learnt to know all the individuals perfectly according to *all* their characters, and have made ourselves thoroughly acquainted with each character in all its relations, that we are enabled to find an expression that shall fully mark and distinguish the individuals of the group from those in that immediately succeeding it. As long, however, as this perfect knowledge is nothing more than a mere desideratum, we content ourselves for the time with the choice of any character that may seem most applicable for the purposes of classification, although it may not be perfectly correct, and may not draw the line as clearly as should be. Thus there will present themselves many individuals which the provisionally adopted character will not aid us in defining, and such we term Transition forms. These exist, therefore, only as the creations of our ignorance; and it is merely owing to our own inefficient knowledge that we are unable to define clearly the different boundaries, the occurrence of these transitions affording us a criterion by which to judge of the great deficiency of our information regarding any one particular point, and thus stimulating us to further and more exact observations.

There still remains a third signification of the word *transition* for us to notice. We have not as yet found any expression for the *nature* of the plant in general, which might enable us in doubtful cases to decide upon the vegetable or animal nature of an object. On passing from one *certain* group of plants to another, we must have common parts of both by which the two groups may be connected together under one general conception of plants, that we may know with certainty that we are not encroaching upon the department of animal life. This occurs everywhere, where we combine two or more subordinate groups within the sphere of a higher conception; and here, consequently, the links necessary to convince us that we are correctly embracing the lower groups under the idea of a higher one must be regarded as transitions from one group to another, although in a totally different sense from the one already alluded to. Instead of the term transition, I shall in the latter signification use the words "intervening stage," limiting the application of *transition* merely to those cases where the line of demarcation cannot be sharply defined, owing to the deficiency of our knowledge on the subject.

## SECTION I.

### THE ANGIOSPORÆ.

§ 79. Plants develope either from a naked cell, or, in the case of Lichens and *Fungi*, from an enclosed and double cell, into such multifarious and indefinite forms that no general character can be

applied to their parts. They have, therefore, no distinct organs. In the less simple plants, merely certain cells or portions of cells, or else cellular groups with a clearly characteristic constant form and arrangement, especially officiate in the formation of new propagating cells, and, therefore, can alone be regarded as organs. The single or complex cell out of which the new individual is developed, I name spore (*spora*); the parent cell forming and enclosing the former, the spore case (*sporangium*); and a number of these combined together in a definite form with the special parts of the plant which enclose them, a sporocarp (*sporocarpium*). Sometimes, also, individual cells or groups of cells assume the form of fibres or laminæ, in order to fasten the plants to the body which supports them (organs of attachment, *rhizinæ*). These plants have been provisionally divided into three groups, the limits of which are still very ill defined. The best characteristic may perhaps be derived from the habitation and the formation of the spores, and we may thus distinguish those growing in the water (*Pl. aquaticæ*) (*Algæ*), from those growing upon any kind of support in the air (*Pl. aereæ*); and these latter may again be designated as *Fungi* and Lichens, according as their spores are formed separately in protuberances of the sporangia, and thrown off with the latter, or numbers of spores are developed in one sporangium which subsequently bursts to discharge them.

The same useless playing with fictions to explain what is perfectly simple and clear in itself, which meets us at every step in the science of Botany, is not absent here. Most botanists have not deemed it sufficiently abstruse to suppose that cells combine in simple plants to produce simple undefined changeable forms, and much senseless matter has been advanced not only concerning the fusing of leaves and stalks, but also about the formation of buds and all appertaining thereto. In the case of the *Marchantiæ*, which belong to a group of plants in which the formation of the stalk and frond is normal, such views, by way of analogy at any rate, might have some reasonable grounds. In the three groups of plants in question, it is, however, a mere childish play of words to speak of stalks and leaves, if we do not understand under the term definite products of the formative force, and prove the actual existence of such: things created by imagination exist, however, only in confused heads, and not in nature, which embraces nothing beyond the actual in space and time.

The expressions already made use of, and which were first proposed by Link (Elem. Phil. Bot. ed. 2.), fully suffice for the description of the *Angiosporeæ*, although they are not clearly defined, and therefore still loosely applied, and we may thus entirely dispense with the diffuse and in part irrational terminology, and that confusion of words which has originated in vanity and a love of innovation.

It is extremely difficult to characterise the three above-named divisions in such a manner as to decide at once in individual cases; and wholly impossible to do so at present, when we are only able to compare individual conditions instead of complete series of development. For instance, it is wholly impossible to distinguish *Undina* (Algæ) and *Collema* (Lichens); *Sphæria, Sporocybe* (Fungi); and *Verrucaria, Calycium*

(Lichens), or *Mycoderma* (Fungi ?) from *Protococcus* (Algæ), by characters belonging to groups, and scarcely even generically. We may separate them more safely by looking at the whole series of development; but even here the boundaries, as especially between *Algæ* and *Fungi*, when the latter grow in water, are confused, and between *Fungi* and Lichens there are at least transitional forms which it is difficult to bring into a definite position.

If we look, on the one hand, at the often naked fruits of the gelatinous Lichens and the species of *Peziza*, and on the other at the *Sphæriæ*, which agree with many of the Lichens, we soon see that no very marked difference can be established between Lichens and *Fungi* from their conditions of consistence or structure. If we join the *Pyrenomycetes* and the *Discomycetes* to the Lichens, which, as far as regards the former of the two, appears in conformity with a natural arrangement, and is not very extravagant with respect to the latter, if we look upon a *Peziza*, for instance, as an *Apothecium* with the thallus (the mycelium) obliterated — the formation of the spores within the sporangium (*Thecæ*) would in that case be characteristic of Lichens. For the sake of the facility which it affords in the treatment of the subject, I shall adopt this mode of subdivision, without, however, laying any peculiar stress upon its importance. To me it appears evident that whoever has accurately observed both groups must see the little value that is to be attached to the difference of the *thallus* (in the *Lichenes*) and the *stroma* (*Fungi*), (owing to a few green cells in the former,) as characteristic of the two groups. One is disposed to assert that all botanists have abstained from placing most *Sphæriæ* and *Hysteriæ* under the head of Lichens solely because their teachers had told them that they were *Fungi*.

We obtain the following divisions from the form of the spores: — Spores which develop themselves (from 1 to 4) in the sporangium according to the second form of cell formation—*Algæ;* spores which to the number of eight to ten are formed in the sporangium according to the first form of cellular formation—*Lichenes;* and lastly, spores developed individually in smaller lateral expansions of the sporangium, separating themselves with it — *Fungi*.

## I. ALGÆ.

§ 80. The propagating cell (the spore) constitutes, in some rare cases, the whole plant (*Protococcus*, &c.). More generally, however, it expands itself during its development to a long, thread-like, often ramifying cell (*Vaucheria*); or it forms, in a manner with which we are as yet unacquainted, many other cells, variously and multifariously arranged, and thus constitutes the plant (*frons* Auctor).

The simplest forms exhibit waving (*Undina*) or straight rows of spherical cells interspersed here and there with whorls of lateral branches (*Batrachospermum*): in other cases the cells acquire the form of cylinders attached together so as to compose longer or shorter filaments. These threads are either simple, or are themselves ramified in various ways so as to constitute a closed net (*Confervaceæ*). These plants generally secrete a definitely formed gelatinous layer, which in the case of the *Nostochineæ* determines the form of the whole plant, while in that of the *Confervaceæ* it constitutes only a membranous investment of the individual threads.

(See Plate II. fig. 7.) The majority swim freely in water, while in a few the spores form in the course of their development a thread-like prolongation, terminated at the extremity in a little disc which adheres to some foreign body (organs of attachment, *rhizinæ*), as in the instance of the *Polysperma glomerata.* In others, again, the cells developed from the spores arrange themselves so as to produce a greater surface (*Ulvaceæ*), which at times expands at one extremity into a small adhering disc, and occasionally appears as a hollow cylinder (*Solenia* Ag,).

Finally, in the most complicated forms the cellular process developed by the propagating cell gives rise to solid structures composed of cells ranged one upon the other; these are either thread-shaped (*Scitosiphon* Ag.), band-shaped (*Laminaria* Lam.), leaf-like (*Delesseria* Lam.), simple, or divided in many ways, or developed alternately in an apparently regular order into thread-like and leaf-like forms (*Sargassum*). The plants are for the most part attached to some place by a disc-like organ of attachment. At times we meet with bladder-like inflations (*Fucus nodosus*) or pedicled bladders (*Sargassum*).

I believe that no system is destined to be so thoroughly overthrown as the one at present established for the *Algæ*, especially with reference to the lower divisions; and it appears to me that at least one third of the species will probably be set aside. Certain it is, that many species are described three or four times according to the different appearance they have presented under magnifying powers of varying strength. Hence it comes that most writers have had little or no conception of the actual structure of plants in general*, and of the *Algæ* in particular, and that consequently a certain distinction between the stages and kinds of formation is impossible. It is at any rate certain that mere stages of development, which have very frequently been described as peculiar species of plants, must fall to the ground as soon as their true character has been recognised. My views on this subject are fully concurred in by Kützing †, who, after thirteen years' laborious study, declares that there are no species, but merely forms, of *Algæ;* and these he has followed throughout the whole course of their development, showing, in many cases by careful observation, although in a confused manner, that they are devoid of an independent existence.

The terminology in use at the present time with respect to the *Algæ* is a mere confusion of words; and as my purpose is simply to throw a

* Phycomater; Gelatina *inorganica* (?), *effusa, granulis* (but surely *cellulis*) *nullis:* or Byssi meteorici: *formationes aëreæ, vegetatione nulla* (?). What this is I cannot decide; but that it can be no race of plant, must, I should think, be evident to every one who has acquired any fundamental knowledge of the nature of vegetable life. And it will, at all events, be acknowledged by every man, even if he be no botanist, that it is a flagrant absurdity to reckon among plants that which is defined as inorganic, and to which is denied the first and indispensable character of plants. "There is a great confusion in synonymy, which can only be cleared up by the careful examination of original specimens. All delineations hitherto made only allow of a partial idea of the real form and species, owing to their being copied from specimens which were not sufficiently magnified, and also owing to their being drawn without the requisite exactness." — *Kützing, Phycologia generalis*, p. 249.

† Phycologia generalis.

glance over the forms as far as may be necessary for the clear comprehension of the whole, and not to furnish my readers with a monography, I may wholly dispense with all these empty terms. Kützing, who has carried this fabrication of words beyond all limits, makes use of seventy terms for the different forms of the family of the *Algæ*.

We have already spoken at large, in the first part of this work (p. 36), of a very interesting specimen of *Algæ*, namely, the Fermentation Fungus. Much has been written of late years upon this subject, but I will here only enumerate some of the principal works: as, for instance, Schwann (Poggendorff's Ann. vol. xli. p. 184.); Cagniard-Latour (L'Institut, 1836, Nov. 23.); Meyen (Wiegmann's Archiv, 1838, vol. ii. p. 99.); Querenne (Journal de Pharmacie, 1838, June); Turpin (Comptes rendus de l'Académ. 1838, July; and L'Institut, 1838, August). We are still very much in the dark respecting the law of development of the *Algæ*. I am not acquainted with any complete exposition of the subject.* There are many *Algæ* of which we do not even know the spores; for where, in the case of the *Confervæ*, the author speaks of a *Massa sporacea* (chlorophyll, starch, &c.), he neither understands himself or nature. Kützing certainly maintains that the granular cellular contents are developed into new plants, but his representations to that effect are far from furnishing us with the requisite proofs; besides, the whole thing is so contrary to all analogy in the vegetable kingdom that it seems best to receive the fact only as provisionally true. The process exhibited in the *Protococcus viridis* is the simplest. Here a spherical cell is slightly expanded, soon after which we perceive two young cells, which become isolated as the parent cell gradually disappears. I have not, however, been able to observe how these young cells are developed. In *Mougeotia genuflexa* (fig. 120.), the cell of the spore extends at one extremity into a tube, whose end bulges out into a spherical form, flattening out on reaching any support in order to attach itself to it (*f*). From the other extremity of the spore, cells proceed, which expand cylindrically and arrange in a thread-like form. I have been unable to trace them in their earliest development; and have hitherto been unsuccessful in my attempts to observe the germination of *Spirogyra*. Since *Vaucher* † observed the young *Confervæ* issuing from the burst spore ‡, nothing more exact has been noticed with regard to

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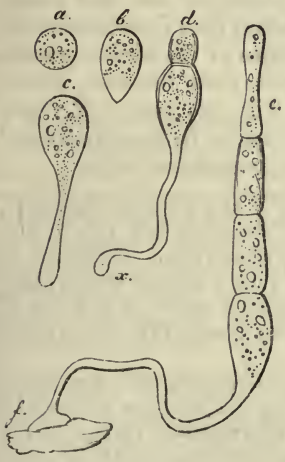


* Meyen, Physiologie, vol. iii. p. 411., gives the heading of his subject as the Propagation of the *Algæ*, but in the text speaks almost entirely of *Diatomeæ*, part of which are undoubtedly animals, and of a few *Confervæ*. The most important, as the *Fucoideæ* and *Florideæ*, are not even mentioned; and this is called a *system* of physiology.

† Vaucher, Histoire des Conferves d'Eau douce. Genève, 1809.

‡ Meyen, Physiologie, vol. iii. p. 423., offers only conjectures on the subject.

120 *Mougeotia genuflexa*. Development of the plant from the spore (*a*) in four stages (*b*—*e*). The last stage shows the adhesion of the plant by an adhering disc (*f*), which is already indicated at *d* by the spherical enlargement (*x*).

them. In a few instances germination has been observed in more developed *Algæ*, as, for instance, by Martius *, Agardh, and Kützing, without, however, their having had regard to the most essential points, viz. the origin of new cells. The self-division so much insisted upon by Meyen † has not been established by observation, excepting in the case of *Diatomeæ*, and other doubtful organisms, but has merely been assumed. In *Hydrodictyon utriculatum* a young plant is developed within a cell in an unknown manner.‡ Mohl § thinks he has seen a multiplication of cells by division in *Conferva glomerata*. We are, however, indebted to Nägeli for elucidating this relation, as well as the whole cellular formation, of the *Algæ*, by showing that all increase of cells in the *Algæ* depends upon the second type of cellular formation (§ 14).

§ 81. In the simplest forms of *Algæ* the plant itself is the parent cell (*sporangium*) of the spores (*Protococcus*). In the thread-like *Vaucheriæ*, a portion of the cell expands spherically into a sporangium. In those composed of many cells the sporangium is formed from one individual cell which, at times swelling into a spherical form, furnishes the sporangium (*Œdogonium vesicatum*). In the case of the greater part, however, we know but little of the formation of the spores. In the more complex *Florideæ* there are apparently two kinds of spores in the different individuals. Some enclosed in large numbers in a sporocarp (Kützing's *Kapselfrüchte*) are developed in a manner with which we are still unacquainted: the others (Kützing's *Vierlingsfrüchte*) are formed, according to Nägeli, exactly like the pollen-granules of the higher plants, in a parent cell (sporangium), which sometimes becomes subsequently absorbed and disappears. ‖ The different forms of fruits are either scattered, heaped together, or again frequently united upon peculiarly formed lobes of the plants (*receptaculum*).

Here, again, we have every thing shrouded in the greatest darkness. Not that the water contains marvels, as Link declares, but that it has been examined with the most unsatisfactory observation, combined in some degree with an unrestrained fancy. In such a state of things there cannot of course exist any thorough well-grounded study of the law of development. I have myself unfortunately been unable hitherto to make any more comprehensive observations.

In certain respects, Kützing's *Phycologia generalis* forms a new epoch in the study of the *Algæ*, and, notwithstanding the constant and reiterated changes and enlargements which he superfluously makes in the terminology, and the deficiency which is throughout observable of accurate observations upon the law of development, his work furnishes us with the first attempt at arrangement of the greater part of the mate-

* Martius, Nov. Act. Leopold. Carol. ix. p. 217.

† Meyen, Physiologie, vol. iii. p. 440, &c.

‡ Vaucher, Hist. de Conf.

§ "Vermehrung der Pflanzenzelle durch Theilung." Multiplication of the vegetable cell by division. Tüb. 1836.

‖ This Nägeli maintains at any rate (*loc. cit.*), whilst Decaisne (Archives du Mus. d'Hist. Nat. vol. ii.; Plantes de l'Arabie heureuse, p. 112.) positively maintains the reverse.

rials, which he handles according to a principle of unity, by which we are enabled to compare separate observations with each other, and trace their mutual relations. And we must not conceal that it is extremely difficult, owing to the external relations, to make comprehensive observations upon the law of development, and that consequently the reproaches which we must make against the state of the science in regard to the *Algæ* in our day, only apply to a certain extent to the individual investigations. In some degree, certainly, the cause lies in the artificial, senseless methods of research that infect the whole science of Botany, which has hitherto directed its attention far more to herbaria than to living plants; and hence, those who live far inland become Algologists, whilst botanists residing near the sea-side busy themselves in describing some little dried *Jungermannia* brought from Java; and European investigators thus too often devote more attention to tropical plants than to those that are indigenous to their own country, and are in their own immediate neighbourhood.

The so-called copulation of *Spirogyra* and a few other *Confervæ* (fig. 121.) are generally represented as especially remarkable. They consist

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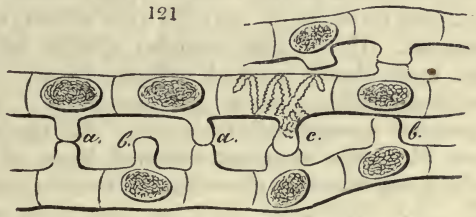



of thread-like cylindrical cells arranged in a linear series. At a definite time one side of each cell expands into a papilla, which combines with any papilla of another cell of the same or another filament with which it may come in contact, and then the partition is absorbed, the contents of the one cell pass over into those of the other cell, and out of the total mass a spore is formed (fig. 121. *a a*). I have observed the following cases, which prove how inessential this process really is. Two cells were combined with the papilla of a third cell; and thus arose four spores, one in each of the first-named cells, and two in the third. Three cells were combined, and the result was the formation of one spore in the space formed by the three papilla. Again: two cells were combined, in the one of which there appeared two spores, and a third spore in the cavity of the papilla. Two cells combined together, and here a spore was formed in each one (fig. 121. *c*). Another instance very frequently occurred in which one cell, that had a papilla which did not combine with another, exhibited a spore formed within the cell (fig. 121. *b b*). Finally, it sometimes happens, although but rarely, that a spore is formed without the cell having borne any papilla.

The *Algæ* certainly merit the most thorough examination, as we are

[121] *Zygnema quininum.* Phenomena of the so-called copulation. At *a a*, the connexion is effected, and the contents, being transferred from one thread to another, form a spore. At *b b*, the projections are formed, without, however, their being able to combine with another cell; notwithstanding which, a spore is formed. At *c*, a spore is formed, and here another prolongation effected, which is connected with another cell, in which the contents begin at the same time to concentrate themselves into a spore.

justified in expecting important results to science from them on account of the simplicity of their structure and life. To effect this, however, it will be necessary, if we would avoid thorough confusion, entirely to exclude the *Diatomeæ* and the true *Oscillatoriæ*, which, according to my view, are equally dubious.

§ 82. The *Algæ* consist generally of cells in a low condition of development, having for the most part gelatinous walls; in the *Fucoideæ* and *Florideæ* we find, in the interior, more elongated or broader cells, which, by their distinct porous canals, indicate the presence of thickening layers, so that the cavity of the cell has frequently a beautifully ramified appearance. These cells are very often found to be arranged with the greatest regularity. In most of the *Algæ*, the tender mucous integument of the inner surface of the cell-wall is especially developed, and here motions of currents of fluid may frequently be traced, as, for instance, in the species of *Spirogyra*. The chlorophyll often appears as an investment of the cell-wall, in the form of spiral bands with jagged edges; the granular contents of the cells (the starch) are generally very coarse-grained. In the more complex species, we may distinguish a smaller, more closely packed cellular tissue, as rind (*cortex*) from the larger-celled porous pith (*medulla*). The vesicles contain very porous, spongy cellular tissue. All the *Algæ* exhibit a more or less distinctly apparent secreted layer of gelatinous, amorphous substance, covering the whole external surface.

The structure of the *Algæ* is, on the whole, very simple, if we do not include amongst them the dubious *Diatomeæ*, &c. with their siliceous shields; and which, as has been already stated, are quite out of place here. I give an exact representation (Plate II. figs. 1 to 6.) of the siliceous shield of *Navicula viridis*, one of the commonest of the *Diatomeæ*, of which I have not hitherto met with so minute, nor indeed any accurate, representation. It will show that this curious structure is wholly without analogy in the vegetable kingdom*, and cannot be derived from laws of vegetation with which we are at present acquainted. One of the most striking phenomena is the deposition of chlorophyll in the spiral jagged bands observed in the species of *Spirogyra*. The formation of a secreted layer upon the surface of the *Algæ* appears to throw considerable light upon the nature of the cuticula in the higher plants. *Cabomba aquatica* shows great affinity to these formations, by its very gelatinous cuticula. It has, however, been shown by the observations of Kützing†, that this layer in the *Algæ* must certainly be a secreted substance, as, when removed or injured, it is replaced by a liquid mucus, that gradually hardens. On the other hand, the clothing of the interior of the actively vegetating cell, with a semi fluid layer of a nitrogenous substance, frequently circulating in currents (inappropriately termed an amylid cell by Kützing), is most remarkably conspicuous in the *Algæ*. Compare, with reference to the above, the Plate II. fig. 7. with the accompanying explanation.

* Meyen passes this by as a matter of common occurrence because silica is found in other plants, and thus entirely overlooks the essential difference.

† Kützing, Phycologia generalis, p. 87.

## II. FUNGI.

§ 83. The spore expands in many directions into an interwoven tissue (*mycelium, stroma, flocci, thallus*) composed of thread-like, mostly transitory, cells, forming the actual plant, which exhibits no other organs excepting those of propagation. We are wont to make the transitory nature of this part a means of judging of the more strikingly apparent, and frequently more lasting propagating organs of the whole plant.

A Fungus, as I believe, very seldom consists solely of roundish cells. I cannot regard the true Uredines, &c. (*Coniomycetes*) as independent plants. Meyen observed the formation of *Uredo Maidis** as an abnormal process of cell-formation in the interior of the cells of the parent plant; and, in this respect, my own observations on *Elymus arenarius* coincide with his: on the other hand, the views of Leveillé † appear but little entitled to be opposed to the investigations of Meyen, being evidently more superficial and incomplete. An advanced stage of knowledge regarding the Fungus tribes will no doubt lead to the general conviction that all *Fungi* consist of a few thread-like cells, forming spores in a similar manner; and that the classification into groups, tribes, and species, must depend upon the modification of the process of the formation of spores, upon the aggregation of individual fungus-cells to more complex plants, and upon the types of the forms of these compound *Fungi*. I must, also, regard many other supposed species of plants, as *Cæoma*, *Puccinia*, &c., as devoid of individuality, and simply as diseases of plants. On the other hand, such *Fungi* as are formed in the intercellular passages, and grow from the openings of the stomates, I consider as real parasitical plants (*Epiphytæ*). The whole tribe of the *Leptomiteæ* Ag. do not appertain as independent structures to the *Algæ*, but to the *Fungi*‡, as being species of mould germinating in water. The confusion that existed regarding these most imperfect plants was, up to the most recent time, beyond all description, and will not be very speedily removed, since only a few botanists deserving of credit, as Leveillé, Montagne, and Berkeley, have devoted themselves to the general study of these groups; and, in spite of the best observations on the subject, the old errors are for ever revived in systematic works. It may be said of such systematisers, as of the French emigrants, "They forget nothing, and learn nothing."§

We still know but little of the law of development of *Fungi*. Thus, although the origin of new cells from the spore may have been observed, we yet have no delineation of any one single kind. J. Schmitz has made a very successful introduction, in recent times, to accurate observations of the law of development. (See Beiträge zur Anatomie and Physiologie der Schwämme, Linnæa 1843, p. 417.)

We have certainly recently acquired many very complete series of

* Wiegmann's Archiv, Jahrg. 1837, vol. i. p. 419.

† Annales des Sc. N., ser. ii. vol. xi. p. 5.

‡ Compare, amongst others, Meyen, in Wiegmann's Archiv, 1838, vol. ii. p. 100.; and Montagne's Skizzen zur Organogr. und Physiol. der Schwämme, Prag. 1844, p. 15.

§ Thus we find in Kützing's *Phycolog. gen.* all the species of *Leptomitus* and *Hygrocrocis* received as *Algæ*.

observations on several of the more interesting species, but even these are deficient, in a botanical point of view, in that completeness which can alone be obtained by the acquirement of a more perfect knowledge of the origin of the individual cells. I will here especially mention the following works:—

1. The Ergot (*Sphacelia segetum*), on which observations have been contributed by Meyen (Müller's Archiv, 1838, p. 357.); Leveillé (Ann. des Sciences Nat. 1837, Dec.); Phœbus (Description of German Poisonous Plants, Part 2, p. 97.); Fée (Flora, 1839, p. 293.); Spiering (*De Secali cornuto* Diss. inaug., Berlin, 1839); E. J. Quekett (Ann. of Nat. History, 1839, p. 54.).

2. The Muscardine (Calcino, *Botrytis Bassiana*); a Fungus growing upon the Caterpillar of the Silkworm, observed by Bassi (Wiegmann's Archiv, 1837, vol. ii. p. 107.); Balsamo Crivelli (Linnæa, 1836, p. 609.); Audouin and Montagne (Comptes rendus de l'Acad. 1838, p. 86.).

§ 84. The development of the organs of propagation varies very much, and has only been perfectly observed in a very few instances.

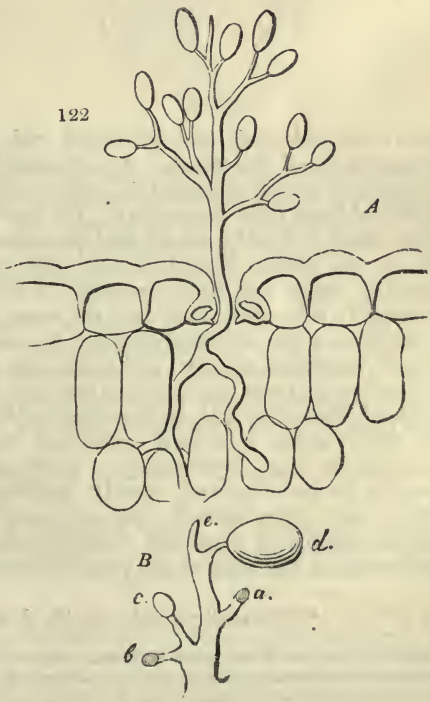
The most simple (*Hyphomycetes*, filamentous *Fungi*) form, at the end of the thread-like cells, narrower protuberances, in each of which a spore is developed; this at length separates, having consequently a double membrane, the cell of the spore itself and the covering (*sporangium*) arising from the parent cell, as, for instance, *Penicillium*, *Botrytis*. In others the thread-like cells form a spherical swelling at the extremity, from which project a number of such prolongations, each of which contains a spore, while the whole forms a divided sporangium, as, for instance, *Mucor*, *Penicillium?*

In others (*Gasteromycetæs*, the ventricular *Fungi*) the thread-like cells combine into pointed, or non-pointed, variously-shaped sporocarps; in or upon which are spores, of the development of which we know nothing. After the scattering of the spores, the thread-like cells often remain as tender wool (in the *Trichiaceæ*), or as a delicate network (*capillitium*), as, for instance, in *Stemonitis*, *Cribraria;* and the external capsule (*uterus*, *peridium*) generally composed of fine filamentous cells, is then dissolved, or bursts in different regular ways, as in *Arcyria*, *Geastrum*.

In the most highly developed *Fungi* (*Hymenomycetes*, membrane *Fungi*), elongated pouch-like cells (probably only the ends of the interwoven filiform fungus-cells, developed into the sporocarps, or cells formed at the ends of these cells) combine by arrangement side by side so closely as to form a membrane (*hymenium*). Some of the cells of this membrane enlarge considerably (*sporangia*), and send out from one to six points at their free extremity, in each of which a spore is developed. The filiform cells of the Fungus then either form round masses, closed in all round (*sporocarps*), with cavities in their interior, the walls of which are clothed by the hymenium, or they form definitely arranged columns (in *Merisma*), tubes (in *Polyporus*), or lamellæ (in *Dædalea*, *Agaricus*), which are clothed by the hymenium (the *Hymenomycetes*). Of the latter we only know, with any amount of accuracy, the law of develop-

ment relating to the Toadstools, and more especially that of the *Agaricineæ*. In these latter there are formed, at definite parts of the floculent mycelium, small hollow heads (*volvæ*); at the bottom of the cavity there grows a corpuscle, shortly pedunculated below, and enlarged into spherical form at the top. In the lower part of this protuberance, a horizontal circular cavity is formed, to the upper surface of which are attached the tubes, lamella, &c., which bear the hymenium. The bottom of the cavity is only formed by a membrane (*indusium*), which is either separated from the pedicle on its further development, or, loosening itself from it and the upper part at the same time, remains as a membranous ring (*annulus*) upon the stalk. The upper part, which supports the hymenium on its lower surface, dilates subsequently, and appears as an umbrella-like expansion, called the hat (*pileus*). The whole then breaks through the volva, which is very soon dissolved.

Almost all the works that have hitherto appeared on the lower *Fungi* are wholly useless, and may, without farther consideration, be cast aside, since the work must again be commenced from the beginning. Investigations are of no value where they do not trace the composition of the forms from the individual cells. Even by the aid of delineations (as, for instance, in Nees von Esenbeck's System of the Fungi and of Flocculent Plants. *Schwämme*), we do not learn whether we have to do with individual cells, or structures composed of such cells; and yet on this depends everything. I must confess that I find it quite impossible to determine one of the lower *Fungi* from the ordinary descriptions, as they do not express what nature exhibits. Even delineations are not often of much avail. This arises from the fact that in many cases the specific difference does not certainly rest in the plant, but in the observers, their instruments, and the magnifying power used. My own limited observations yield the following results: on the *Allium fistulosum* there is, on the yellow leaves, a small epiphyte (*Botrytis?*) (fig. 122.), consisting of one single multifariously ramifying cell. It germinates in the intercel-




[122] *Botrytis* (*parasitica?*). *A*, Grown out from the stomate of a leaf of *Allium fistu-*

lular passages, and grows as a little stem from the stomate, branching externally in a tree-like form. I observed it in all its stages of development from the germ. At the points of the branches, and distinctly enclosed by the membrane, a small cell is seen, which gradually swells to a considerable size, and then separates itself from the branch with the integument it has derived from the parent cell. This is the mode of formation of the spore. According to Meyen's delineations*, the same process goes on in *Penicillium*. I found upon damp linen a colourless mould (*Mucor?*) (fig. 123.), consisting of one cylindrical cell (seldom more), much ramified upon the surface; it had one stem, the end of which was

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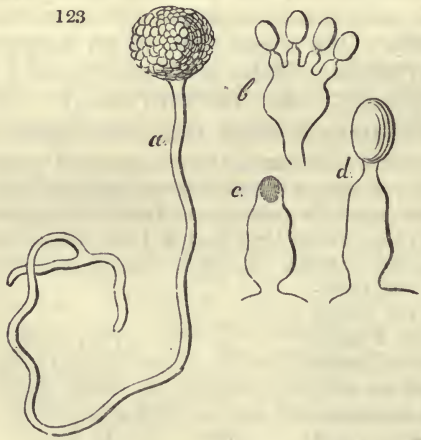


spherically enlarged, and furnished with small pear-shaped processes, projecting in all directions. An individual cell was distinctly visible in the interior and at the point of each process, which, gradually enlarging, separated itself from its support. On the withering leaves of the *Passiflora alata*, I found a mould that was almost as black as pitch, consisting of one simple thread, formed below of shorter and thicker, and above of longer and narrower cells, of which the uppermost, which was spherically expanded, exhibited the same process of spore-development. I found upon the withered stalks of the same plant another whitish-gray mould, composed of short and thick cells at the bottom, and longer and thinner ones at the top, forming ramified threads. The two or three last joints of the stalks and the branches contained a turbid, mucous, granular fluid, which sometimes exhibited very small but sharply-defined globules, or discs (cytoblasts). Very minute delicate cells were frequently to be observed, closely applied upon the wall of the cell, which was often arched outward over the cells. I met with all possible stages of transition from this condition to a longer wart-like projection of the wall, at the point of which lay a young cell, free and

* Pflanzenphysiologie, vol. iii. pl. x. figs. 22. 20, and 21.

*losum.* A section of the latter is given. *B*, A portion of the fungus, with spores in different conditions of development (*a*—*d*), and a barren branch (*e*).

[123] *Mucor* (*sphærocephalus?*). *a*, The whole plant. *b*, The head of the spore-case, in a longitudinal section, the greater part of the processes with the spores being omitted in the delineation. *c*, Earlier condition of such a protuberance, with the spore originating from it. *d*, Protuberance, with the ripe spore.

again from this condition to that of a riper spore, connected by a short pedicle with the cellular wall. (Compare Plate II., fig. 8.) In both of the above-described species of mould, the lowest cell was short, almost barrel-shaped, and immediately attached to the still distinctly recognisable cells of the epidermis of the plant, which, although they were withered, were otherwise wholly uninjured, while not a trace of adhering discs or fibres was to be perceived. I likewise observed upon the hymenium of *Agaricus campestris* (figs. 124, 125.) and *A. Oreades*, and *Amanita*

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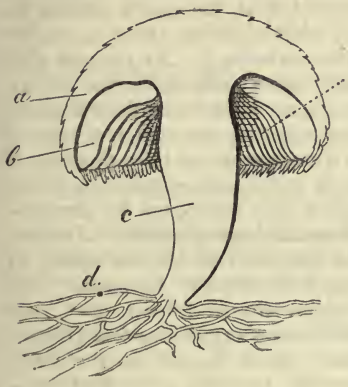


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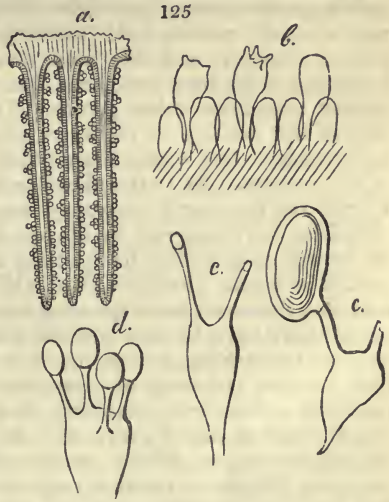



*muscaria*, the perfect formation of these processes from the large cells of the hymenium, and the origin of the spores as little globules within the points of these projections. On comparing this representation with what follows, it will become very evident that the external membrane of the Fungus-spores cannot be compared with that of the Moss-spores, or the pollen granules; but that it represents a spore-case. This membrane does not prevent the spore from expanding irregularly, in the act of germination, into many thread- like prolongations, and that at any point indiscriminately. The above-mentioned development of the pileus of the pileate *Fungi* has been thoroughly observed, and frequently delineated.* Of the development of all other *Fungi*, with the exception of the

* By Bischoff, among others, Handb. der Botanik, pl. vii. fig. 163. of *Agaricus volvaceus*.

[124] *Agaricus campestris*, shown in a longitudinal section. *a*, Substance of the pileus. *b*, The lamellæ, covered by the hymenium. *c*, The stipe of the pileus. *d*, The actual plant (mycelium). The dotted line indicates the direction of the section 125. *a*.

[125] *a*, A section through the lamellæ of the pileus of the *Agaricus campestris* (fig. 124.). The lamellæ are covered by the hymenium, on which appear the spores. *b* is a portion of the hymenium, with the spore-cases in three different stages of formation; the middle one shows already the four processes. *c*, A spore somewhat more developed. In the process to the right is a spore in the first stage; to the left, one somewhat more developed. *d* shows a spore-case with four processes and many half-developed spores. *e*, The upper part of a spore-case, with a process, and a fully developed spore.

parasitical*, we know scarcely anything. In the *Fungi*, too, we observe a formation of the spores very similar to the copulation in *Spirogyra;* with this exception, that here the spore is developed quite regularly in the middle of the tube formed by the fusion of the two papillæ.†

In more recent times, much has been said on the subject of the antheridia of the *Fungi*‡; and Meyen § has even discovered them in *Æcidium.* What is to be thought of all this scientific juggling with the word anther, will be subsequently discussed. The case is as follows in the *Hymenomycetes.* Beside the sporiferous cells, between the sterile cells upon the hymenium, there are a few projecting, wider tubes, filled with a turbid, mucous fluid (*cystides*, Leveillé; *utricles*, Berkeley; *paraphyses*, Auctor); and this is all that we know of the matter. Klotsch, according to his own statement, has observed that the spores coming in contact with these tubes germinate more certainly than those in which he was not positive of the same condition existing.‖ At present this seems to be a very vague supposition, and proves nothing for the nature of the anthers. As to the *Æcidium* anthers, an exanthema described by Unger, and frequently occurring, together with the external eruption of *Æcidium*—it is asserted by Meyen, that a more accurate investigation of its formation, as well as its relations in time and space, *compel* him to regard it as a male *Æcidium* plant, although it may be proved by observation that there can be no question here of actual impregnation. Anthers must really have become a fixed idea in the mind of Meyen, since, in spite of everything, he can declare these structures to be such. The facts furnish not only no compulsory arguments in favour of it, but not even a shadow of possibility, that *Æcidiolum exanthematum* (Ung.), which develops *alone* previously, frequently upon leaves, on the *other* side of which the *Æcidia* are formed, while sometimes no such consequence follows, — stand in any other relation to the *Æcidium* than the *Acne punctata* does to the *Acne rosacea,* in the human subject, or any one disease of the skin to another. Those imaginative physicians who declare disease to be an independent organism, have, according to this analogy, a wide field for the flights of their fancy, in seeking for males and females among the different pocks, pustules, and vesicles.

§ 85. Filiform cells and the interwoven tissue are almost the sole element of the *Fungi.* The nature of the cells, however, varies from a readily deliquescent softness, fatty or greasy, as it were, to the touch, to the most compact wood-like hardness, as in German tinder. Spiral formations do not appear to occur. A few *Agarics* contain a milky juice, which, in the case of the *Ag. deliciosus* at least, is contained in definite small groups of parenchymatous cells.

The hair-like cells in the sporocarp of the *Trichia* and the *Arcyria* appear almost like spiral fibrous cells; but I think that I have reason to assert that they are merely flat band-like cells spirally twisted. In the

* See Unger's excellent treatise, Die Exantheme der Pflanze, Vienna, 1833.

† See Ehrenberg, in Transactions of the Ges. naturforschender Freunde, Berlin, 1820, vol. i. page ii.

‡ See Wiegmann's Archiv, 1839, vol. ii. p. 51.

§ Pflanzpathologie, p. 41.

‖ Dietrich's Flora of the Kingdom of Prussia, vol. vi., under the head *Agaricus deliquescens.*

*Ag. deliciosus* the milky juice is certainly present, as I have indicated; but some have insisted that they also found true lacteals in *Fungi*,—a statement that for the present I must leave undisputed. The most remarkable thing in the *Fungi* is at all events the great difference in the nature of the cell-membrane, which, at least, according to Payen's investigations, consists of common cellulose. The state of decomposition into which the various species of *Coprinus* pass in the course of a few hours, becoming converted into a black, highly carbonaceous fluid, is very striking indeed. But we are still deficient here in accurate observations. *Telephora hirsuta* contains, according to Schmitz (Linnæa, 1834, p. 438.), beautiful octoedric crystals (oxalate of lime?)

## III. LICHENES (Lichens).

§ 86. Whilst the *Fungi* form their spores in a thread-like prolongation of the parent cell, and separate by constriction across the neck, the Lichens develope many spores simultaneously (many of them double spores) in the interior of a larger parent cell. We thus have a clearly defined limit drawn between the two groups.

Many nuclear *Fungi* (*Pyrenomycetes*) cannot, or at least not easily, be distinguished, without previous acquaintance with them, from many Lichens (as, for instance, of the groups *Idiothalami* and *Gasterothalami*). They correspond so closely with Lichens, with respect to the law of the development of their spores, that I, at least, for my part am unable to separate them. But the same may be said of the discoid *Fungi* (*Discomycetes*). Most of the smaller species of *Peziza* are altogether deficient in any characteristic by which they may be distinguished from the apothecia of Lichens as a peculiar order, especially if we compare with them the soft gelatinous substance of the fruits of the *Collema*, which so frequently occur without any thallus. I therefore combine them with the Lichens, as I thus gain from the peculiar, essentially-distinct history of their development a well-marked characteristic to separate the two groups. After the admirable observations and investigations of Camille Montagne*, we can no longer doubt that *Lichina* (*Ag.*) belongs to the true Lichens.

§ 87. The spores of Lichens develope, in a way of which we are ignorant, cells mostly of roundish form, which spread out flat upon the subjacent surface (*protothallus*): by degrees larger globular cells are formed upon this, which the upper and under surfaces, becoming more closely connected, and the lower face a little elongated in a vertical direction, form a plant (*thàllus* Aut.) of crustaceous aspect (*thallus crustaceus*), the outline of which appears usually very irregular and dependent upon accident.

In other forms the Lichen tissue is developed between the upper and lower layer, and then the plant assumes more definite and independent lobed forms (*thallus foliaceus*), the outline of which is generally circular. Irregular bundles of interwoven tissue often separate themselves from the lower surface, serving as organs of

* Ann. de Sc. Nat. 1841, xv. (Mars), p. 146.

attachment (*rhizinæ*). For the most part the *thallus foliaceus* is more or less closely appressed to the supporting surface, sometimes only fastened at the middle point by a small adhering disc (as, for instance, in *Umbilicaria*); at others it rises freely, and then appears in flat ramifying forms, which always admit of being distinguished from the succeeding form by the inequality of their two surfaces.

Finally, in the highest forms the cellular mass rises and forms multifariously ramifying bands or threads of greater or lesser thickness (*thallus fruticulosus*).

We know but little as yet of the law of development of Lichens. Hitherto, Meyer* and Wallroth† are the only ones who have given us any information on the subject; yet both were as deficient in fundamental physiological information to know what was requisite, as in good microscopes, &c., to see things worthy of being noticed. Meyer has clearly and fully explained all that could be seen with the naked eye, whilst Wallroth has rendered his work wholly unendurable by the use of a terminology as superfluous as it is disgustingly barbarous.

The structure of the forms in Lichens is on the whole very simple. As they almost all grow uniformly from one point of the spore in all directions, and are besides generally attached to the supporting surface, the most general is the round outline, modified by the form of the surface on which they grow, and by the specific structure of the lobes. In some, as, for instance, in those nuclear *Fungi* which I include under the same head and *Helvellaceæ*, and also in many true Lichens, especially in the pulverulent Lichens, or as, for instance, in *Coniothalami*, and some columellar Lichens, the plant is so perishable that we scarcely find anything beyond naked sporocarps. In some, as in the *Graphideæ*, &c., the plant, similarly to what is the case in most *Pyrenomycetes*, expands itself within those parts of plants (mostly bark) which serve as a basis to it, and subsequently, after the destruction of the covering, nothing appears but the naked sporocarp, or sometimes, but rarely, also the plant itself. It is only in a very few cases that the plant rises stem-like and free from the base, either by the erection of the lobes, as in *Evernia*, *Borrera*, &c., or by some real difference of development, where the plant developes linearly upwards instead of laterally and superficially; thus, consequently, exhibiting the same surface as it had previously done while recumbent. The word *thallus* is superfluous in the case of such a plant.

§ 88. The development of the spores is very uniform for all cases included within the limits of this family. At wholly indefinite parts of the surface of the plant, there is formed a semi-circular channel-shaped, or more or less spherical or cylindrically closed layer of delicate walled, closely packed, roundish cells, which sometimes appear coloured, as in *Lecidea sanguinea* (when forming a rim round the developed sporocarp, named *excipulum proprium*); and on the inner surface of this layer is a second, composed of thin filiform cells (*paraphyses*, Saftfäden), placed vertically upon the preceding layer (*lamina proligera* Auct.). By degrees,

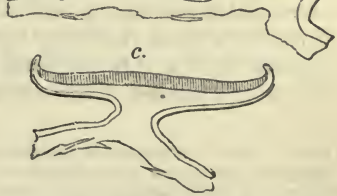
* The Development, Metamorphosis, and Propagation of Lichens. Göttingen, 1825.
† Natural History of Lichens. Frankfort, 1825–27.

single, broader, elliptical, tender-walled cells (*sporangia, thecæ, asci,* Auct.), grow up between them, and soon become filled with a viscid matter. Within these, cell-nuclei are developed, and from them cells which form simple spores; or, again, two or more cell-nuclei appear, from which cells, and then *double-spores*, are developed. During this process, the whole sporocarp approaches by degrees nearer to the surface of the plant, being always covered by a substance the tissue of which it is difficult to determine, but which appears to be partly the product of the *paraphyses*, frequently occurring as a black, finely granular, mass, as is especially the case in *Pyrenomycetes* and *Pyrenothalami;* and partly, in the subsequently expanded fruits, composed of a thin lamella of the cortical layer of the thallus, and is sooner or later destroyed. Remaining in this closed condition as a nucleus, it forms the fruit of *Pyrenomycetes* and *Pyrenothalami* (*sporangia angiospora nucleo prædita*, Meyer). In others it bursts through the upper surface, spreads itself more or less into a linear cup, or disc-shaped (*apothecium*) *patella*, when circular; *lirella*, when linear; (*sporocarpia angiospora laminam gerentia*, Meyer). It sometimes raises a part of the upper surface of the plant, which then appears as a margin (*margo thallodes, excipulum thallodes*); at others, again, this portion grows more decidedly out, and raises the sporocarp upon a pedicle (*podetium*) varying in height. In most Lichens the sporangia remain long closed; in some, however, they open early, and the spores then lie free upon the sporocarp (*sporocarpia gymnospora*, Meyer; *coniothalami*).

The history of the development of the fruit of the Lichens is still very incomplete. Meyer has furnished us with much valuable information concerning all that may be seen by the naked eye, or an ordinary lens; as, for instance, his valuable account of the development of the cup-shaped fruits of the species of the *Cladonia*, appearing either on the margin in new fruits, or expanding into cups. I have sketched the process from my own observations on *Borrera ciliaris, Lecidea sanguinea, Sphærophoron coralloides, Calycium trachelinum, Parmelia subfusca*, &c. By way of illustration I will here give the development of the sporocarp of *Borrera ciliaris* (figs. 126. 127.), and at Plate II. fig. 9.

126

127




[126] *Borrera ciliaris;* a portion of the plant. *a*, First beginning of a sporocarp. *b*, The same more fully developed. *c*, Quite developed.

[127] Section through the sporocarp of the *Borrera ciliaris*, in three different conditions

the development of the spores of the same plant. It is certain that there is no difference perceptible between the development of the pulverulent and that of other Lichens; and equally certain, that the so-called paraphyses appear earlier than the sporangia, and that the latter grow between the former, differing in their volume from the very beginning, which proves that these paraphyses cannot be regarded as abortive sporangia. Finally, it is evident that nothing appears in the whole sporocarp but the paraphyses and the sporangia in different stages of development. We cannot, for want of the necessary details, determine what is meant by the so-called *antheridia* purporting to be discovered by Link (indeed the statement rests only on an announcement in the Prussian newspaper, Die preuss. Staatszeitung). The development of the spores is very interesting in *Lecidea sanguinea*. The young sporangia have a very thick gelatinous wall, and the narrow cavity is filled by a mucous mass (appearing in all Lichens), resembling intestinal convolutions, in which from eight to twelve young spores are formed; of which only one, or occasionally two, are perfectly developed. In time there appears upon the gelatinous wall of the sporangium a thicker, more internal, lamella, formed probably by the pressure of the expanding contents, which is gradually pressed outwards, and at length becomes so blended with the outer bounding surface, that it alone encloses the ripe spore. The ripening spore has likewise a gelatinous cellular membrane, thickened in layers. The abortive, or more or less developed spores often adhere to the perfectly formed spores, imparting to them horns, points, or other strange excrescences. A few Lichen spores have distinctly an outer coating of a hardened mucous substance. In *Parmelia parietina*, for instance, this covering forms hollow hemispheres, covering both ends of the spores, connected by a narrow strip of the same substance (similar to the pollen-granules in *Pinus*). In *Borrera ciliaris* the spores are of a dark, blackish-green colour, and it is difficult to determine whether this is produced by a similar coating, or is due to the cellular contents. Owing to the almost general unanimity that exists as to the use of the terminology, which is, to a great extent, superfluous, I have given the most commonly used expressions in parentheses.

§ 89. The anatomical structure of the Lichens is, generally speaking, very simple. The most complicated, as, for instance, *Borrera ciliaris*, consist of a three-fold layer. The principal mass is formed of lichen tissue; long, thin, dry, mostly forked, ramified, and rather loosely interwoven cells (medullary layer), which curve outward on the external surface, and, by degrees, pass into shorter cells more closely packed together, and firmly connected by much intercellular substance, and often into detached cells, the character of which is with difficulty to be recognised as that of cells at all (*cortical layer*). On the limit between the two lie larger or smaller groups of roundish cells, containing chlorophyll, and exhibiting, in

(*a*, *b*, *c*), which correspond with the parts delineated in fig. 126. at *a*, *b*, *c*. We may distinguish the layers of medullary and cortical layers of the plant in the sporocarp, the layer of spore-cases at *a* still as the nucleus, and as a disc at *b* and *c*. Around the nucleus at *a* there is a delicate layer of formative cells, which at *b* forms a base below the tubular layer. At *a* the whole is enclosed in the layers of medulla and cortex; at *b* the latter layer only covers the disc; at *c* this has also disappeared.

most cases, a distinct cytoblast. The colour of the plant, in a moist condition, depends upon whether the colour of the chlorophyll be yellow (as in the *Parmelia parietina*), brownish (in *P. stygia*), or of a pure green colour (in the *Borrera ciliaris*), &c. since the gelatinous cortical layer is then transparent. In a dry state the colour is more or less blended with gray, according to the different thickness of the cortex. If we suppose two Lichens of the above-described structure laid together by their under surfaces, we have the structure of the flat upright Lichens, as the *Cetraria*, of which the filiform *Usneæ* and *Alectoriæ* are the thinnest forms. The sporangia of all Lichens, with the exception of those plants I have added to them from the *Fungi*, are formed of a substance (starch?) which is rendered blue by iodine. In the *Cetraria islandica*, the cells and the intercellular substance of the cortical layer are coloured blue by iodine (moss starch). In Lichens with a crustaceous thallus, the Lichen tissue is more or less frequently wanting, being replaced by more gelatinous cells, but slightly elongated, and mostly placed vertically upon the base. In the *Pyrenomycetes* we find thin-walled, closely compressed, polygonal cells, as in the *Sphæria fragiformis;* in the *Helvellaceæ* a loose, soft, interwoven tissue. Finally, the gelatinous Lichens consist of convoluted filaments, composed of spherical cells containing chlorophyll, and imbedded in a softish gelatinous intercellular substance, so that it is not possible to distinguish them anatomically from the species of *Undina*.

Lichens offer little worthy of notice. No trace has as yet been discovered of a spiral deposit layer. The thickened walls of the spores of the *Lecidea sanguinea* give, however, indications of this arrangement. Knotty deposits, projecting irregularly into the cavity, are exhibited by the long cells of the *Peltidea canina*. We have a special treatise by Körber* on the green, round, cells; and our only regret is, that the author should have adopted, and even enlarged upon, the terminological waste of words introduced by Wallroth. Special stress is laid upon the conditions under which these cells increase, become somewhat altered, break through the cortical layer, and then appear as masses of dust (*soredia* Auct.) upon the surface, whence the individual cells are distributed and grow into new plants. This is no peculiar property of Lichens, and not a process to be compared with the formation of buds in the higher plants, but simply an evidence that, under favourable circumstances, every vital vegetating cell of a plant may grow into a plant; and of this we shall have occasion, as we proceed, to observe many cases in point. There, as here, a strict individualisation of each cell is at variance with the regular formation of organic fructification, since, in the latter, the individuality of the separate cells appears most circumscribed and checked.

* De Gonidiis Lichenum. Berlin, 1839.

## Appendix.

### CHARÆ (Characeæ).

§ 90. The small group of the *Characeæ*, consisting of the two species *Chara* and *Nitella*, which are separated merely on anatomical grounds, have hitherto presented great difficulties in the way of its classification. It is not improbable that subsequent investigations or discoveries may throw some light upon its proper affinity with other classes. According to our present knowledge, we must, at all events, place it as far from the sexual plants as from the *Algæ*, while we are as yet unable to decide whether it belongs to the *Gymnosporæ* or the *Angiosporæ*.

Here, again, we suffer from the absence of the necessary investigations, especially with regard to the structural formation of the spores. The inexplicable organs, termed anthers, which it presents, afford an analogy, although but a faint one, with structures called antheridiæ in the Mosses and Liverworts. The differences are, however, numerous and important, and we are, as yet, unacquainted with anything analogous to the structure of the sporocarp.

§ 91. The spore-cell, which is enclosed by other cells, expands at a certain definite point, issues from its case, and developes in two directions, terminating downward in one or more thread-like adhering fibres, by which it attaches itself, and upward in an utricle of variable length; from the extremity of this new cells are developed, and there arrange themselves to form the plant.* In *Nitella* the plant consists of separate cylindrical filamentous cells, arranged end to end; at the points of union a whorl of similarly united cells is produced, forming lateral branches, which, on the side turned towards the axil, bears small cells, frequently occurring in pairs, which are likewise inserted at the junction of two cells of the branch. The same arrangement occurs in the case of *Chara*, excepting that here a simple layer of elongated cells is spirally wound round the cells of the axis and the lateral branches, forming a kind of cortical layer. In the cells of *Nitella* and the cortical cells of *Chara*, the chlorophyll granules are ranged in rows, running spirally round the axis of the cells.

The structure of the *Characeæ* is, as has been described, extremely simple. Much, however, is still wanting in regard to our knowledge of individual points. Meyen's account of the development of the cell of the *Characeæ*† scarcely furnishes us with the most superficial information on the subject; and, for an investigation of the kind, it would have been far better had he made choice of a germinating *Nitella*, instead of

* See the admirable treatise of Kaulfuss upon the germination of the *Characeæ*. Leipzig, 1725. [See also a paper on the structure of the *Charæ*, by Mr. Varley. Mic. Trans.—Trans.]

† Meyen's Physiologie, vol. iii. p. 339, &c.

the more complicated *Chara*, as the object of his examination, the former affording an example of one of the simplest cases of this kind of germination. In some species we find, instead of branches inserted in a circle, short thick cells, which, however, are also placed in a whorl, and filled with large starch-granules, and from these new plants are developed under favourable circumstances. We certainly cannot call these buds (§ 93.). As the plants grow entirely in water, every cell having an independent vitality, as it were, the plant increases upwards as it is constantly decaying below, and hence there can be no trace of any root-like development. In the axils of the branches, where also a few spherical cells exist, repetitions of the whole plant (buds) are formed from newly generated cells, and, on the plant dying off to one of these spots, each new plant generated from one of the buds is independently developed. As, in the stage of which we speak, there is, of course, no difference to be perceived between stem and frond, the word "bud" can only have a general signification, and not the more definite meaning which it acquires in the *Gymnosporæ*. Of the motion of sap in the cells of the *Chara* we have already spoken (§ 40.).

A treatise on "the development of the *Chara*, by Karl Müller," (Botanical Journal of von Mohl and Schlechtendal, 1845. p. 393.,) which appears to be a most carefully written work, unfortunately did not come into my hands soon enough for me to do more here than call attention to it.

§ 92. On the lateral branches, generally in the axil of the above-mentioned pair of cells, five cells may be seen spirally wound round a thick mass, and having their parallel extremities surrounded by a kind of pentagonal crown. From this thick granular mass, a large cell (*spore*) is formed, filled with large granules of starch, mucus and oil globules, and with a substance that closely invests the spore-cells, and, from being at first transparent, subsequently becomes green or red, and finally black. The five investing cells then either become cartilaginous, and remain until the whole decays after germination; or they are converted into a gelatinous state, and then speedily dissolved after the sporocarp has fallen. Close below this sporocarp there may generally be seen, at the same time, seated upon a short cylindrical cell, another cell, which is at first simple and spherical, but from which eight (qy. always eight?) cells are gradually developed, which become flattened, and enclose a cavity that appears from its origin to be filled with a dense grumous mass. The eight cells expand into closely compressed radii, arranged side by side, increasing the circumference and depth of the whole body, whilst red granules are gradually deposited upon their inner wall. The dark contents are meanwhile developed into other cells, so that in the perfect organ a conical cell projects, from the cell forming the pedicle, into the cavity, and a cylindrical cell is formed from the middle of each of the eight cells of the wall. These new cells, which likewise contain pale-red granules, bear on their free extremity several spherical or truncated cylindrical cells, from which project many long filaments composed of minute cells. The spherical cells and the filaments

form a dense coil in the centre of the cavity. In each separate cell of the filament we at first see a grumous mass, which, however, subsequently disappears, giving place to a spiral fibre coiled up in two or three turns, and which manifests a peculiar motion on escaping from its cell. These mysterious organs have, as yet, without any reason, been termed anthers.

By way of illustration, I take the reproductive organs of *Chara vulgaris* (fig. 128.). We are still, unfortunately, deficient in the perfect investigations necessary to elucidate the development of these spores; consequently,

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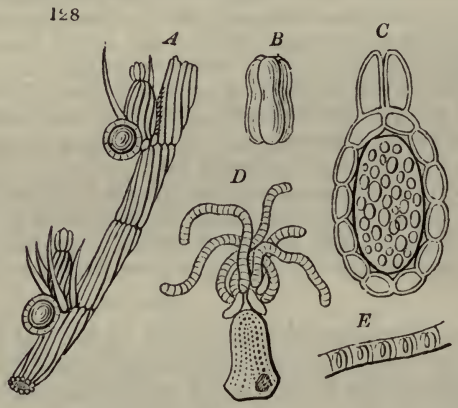



explanations are out of the question in the present case. We possess, however, the valuable results obtained by Fritsche* from his admirable researches into the nature of the so-called anthers (*antheridia*); although there remains much to be done here in tracing the mode in which the cells originate. Thuret † has written a treatise upon the spontaneously moving spiral fibres (which there is a disposition amongst botanists, although without the slightest foundation, to call *spermatozoa*), he discovered two delicate moveable cilia attached to these formations, which have also been since observed by Amici.‡

## SECTION II.

### THE GYMNOSPORÆ.

§ 93. The plants are developed from a cell generally invested by a special membrane, except a few of the Liverworts, in such

* Fritsche on the Pollen, St. Petersburgh, 1837, p. 9.
† Thuret, Ann. des Scienc. Nat., vol. xiv. August, 1840; Botanique, p. 65.
‡ Amici, Flora, Aug. 14. 1844, No. 30. p. 516.

128 *A* is a branch of *Chara vulgaris*, with sporocarps and anthers (*antheridia*): two of the small lateral branches have been cut off from the upper pair. *B*, Early structure of the sporocarp, composed of five parallel cells. *C*. Ripe sporocarp, cut longitudinally; the inner cell (spore) is filled with starch. *D* is a part of the contents of the antheridia. *E*, Cellular filaments, with the moving spiral fibres.

a way that the cell, expanding into a longer or shorter tube, protrudes one extremity at a definite place from the spore-membrane; from this extremity the new plant is gradually developed by the formation of new cells, whilst the other end decays and dies with the membrane of the spore.

On examining the conditions, unbiassed by any previously conceived opinions, we shall perceive that there can be no more striking analogy than the one presented between the germination of the spores of the *Cryptogamic* stem-plants, and the behaviour of the pollen-granules of the *Phanerogamia* upon the stigma, even as the history of the development of the spores and the pollen-granules, no less than their structure, are almost wholly identical. It seems to me, that nothing but a mere cleaving to acquired prejudices, and not a simple observation of nature, could lead to the discovery of an analogy between the sporocarp and the phanerogamic fruit, or between spores and seeds. I can readily believe that it may be difficult to people grown old in such opinions to renounce them, and arrange all their preconceived knowledge in accordance with these newer views, especially where they are not themselves the founders of the new truth; and I have not, therefore, flattered myself with the hope of meeting with a speedy recognition of the truth of my theory of the propagation of the *Phanerogamia*. These prejudices will, however, in part vanish when the matter is exhibited in its entire connection; for even if my views were not based upon direct observation, but were a mere hypothesis, it must be admitted that it was well devised, since it removes the enigmatical separation between *Cryptogamia* and *Phanerogamia*, and at a point where a higher unity is first to be expected, and explains the most widely differing facts from one natural law instead of from two. This simplification of the grounds of explanation is, however, one of the most important methodic claims of a sound natural philosophy. It will be sufficient here cursorily to point out the general results; their special development must be deferred till we treat of the individual groups.

§ 94. The main morphological distinction of the *Gymnosporæ* and the *Angiosporæ* is found in the formation of an axis (stem, *caulis* Auct.), and leaves (*folia*), of which the latter, for the most part, dying off and formed anew, contain the actual vital parenchyma, the former only an essential elongated cellular mass, connecting the leaves and contributing to their nutrition; while (with the exception of the still imperfectly investigated Mosses and Liverworts) the leaves are exclusively the agents of the formation of the propagating cells, the spores and the pollen-granules.

Although an examination of the difference between leaf and stem in this group of plants will justify us in considering it as very marked when compared with accidentally similar forms in the preceding orders, for instance in *Sargassum*, it is still extremely difficult, if not impossible, to base the distinction upon morphological grounds; we must, therefore, do the best we can, and not even disregard physiological indications, such as will be adverted to in the course of the paragraphs. The cause of this is evidently owing to our not possessing any morphological history of development of the *Agamæ*, and, consequently, no sound basis,

as we have obtained in the case of the *Phanerogamia.** We cannot, therefore, as yet express a common law for the peculiar relation existing between leaves and propagating cells, owing to the difficulties which have hitherto presented themselves in Mosses and Liverworts. For the rest, it appears tolerably easy to bring this law into harmony with the nature of the stem and leaf. The latter alone contains, especially, the perfect living cells, in them alone the nutriment that has been taken up is specially concentrated; consequently it is peculiarly here that a sufficient quantity of assimilated matter can be formed to bring about an organic crystallisation, cellular formation; and it is only in these cells that, under the circumstances of the quantitatively limited growth of the leaf, such an amount of assimilated matter can be accumulated as to bring them into a position to begin an independent process of vegetation.

Here, for the first time, we meet with a special formation of organs, since a morphological distinction is produced in the process of development, and we find, on the one side, a quantitatively unlimited stem or axial part, and, on the other, a limited lateral part; that is to say, in the former the axis or stem, in the latter the leaf. To this we may add in the higher groups, another separation of the stem into *stem* in a more limited sense of the word, and into *root*, depending upon the distinction between the opposite directions of the unlimited and continuous development of the stem part, or axis.

§ 95. The *Gymnosporæ* are essentially distinguished, in an anatomical point of view, by the formation of vascular bundles in the stem or in the leaves. The individual development of the separate cells belongs also to a very far higher stage, since, with the exception of the Mosses, we everywhere clearly distinguish spiral thickening layers. Finally, there is no group in which we do not meet, in the separate species or parts of the plants, with a perfectly developed epidermis with stomates.

I have already remarked above (§ 26.), that I see no reason why we should not apply the term "vascular bundle" to the circle of elongated cells in the stem of the Mosses and Liverworts, since it has a similar position and exercises similar functions, if we compare it with the vascular bundles of the *Phanerogamia* without the so-called spiral vessels, as, for instance, in the *Ceratophyllum*, which has likewise a similar anatomical structure. The bundles of elongated cells establish a striking anatomical distinction between *Gymnosporæ* and *Angiosporæ*, nothing bearing any resemblance to them appearing in the latter. The considerable development of the spiral thickening layers forms a no less special difference between these two groups, and it is remarkable that there is not a trace of this formation to be met with in Mosses.

## A. Asexual Plants (*Pl. agamæ*).

§ 96. The *Agamæ* present three stages of development: — 1. The Liverworts form the transition from the *Angiosporæ* to the

* What requires to be essentially specified concerning stem and leaf must be deferred till we treat of the *Phanerogamia*, and then our remarks on the subject will be perfectly applicable to the *Agamæ*, except in the cases where previous notices of the latter make limitations necessary.

*Gymnosporæ.* The propagating cell is usually either wholly developed to a new plant, or it remains partially in the external membrane and dies off. 2. In the remainder, the propagating cell is developed into tubular utricle, one of whose extremities remains in the outer membrane of the spore, and decays afterwards, whilst at the other end cells are formed, which range themselves into a peculiar formation (the germ, *proembryo*). At one part of the latter, a stem-likes tructure is developed from a denser group of cellular tissue; and from this a bud, if we may use the word, arises, from whence the new plant is unfolded. Here, however, this essential difference presents itself, either (*a*) that this axial structure is only capable of development in an upward direction, as in the rootless *Agamæ* (the Mosses and Liverworts), or (*b*) that it is developed both upwards and downwards (*Agamæ* with roots, — the remainder, Linnæus's *Filices*, with the exception of the *Rhizocarpeæ*). All agamic plants present the remarkable peculiarity of having the sporangium absorbed soon after the development of the spores, which always occur in a quaternary combination *, so that the ripe spores remain free in the sporocarps. They differ essentially from the *Angiosporæ*, their distinction from which is further grounded on the equally important resemblance presented between the sporocarps and the anthers of the *Phanerogamia*. On this account the sporangia are generally termed parent cells.

The Conferva-like proembryo in the rootless *Agamæ*, and the Ulva-like proembryo of the others, afford a characteristic by which the groups are most intimately connected; whilst the Liverworts approximate on the one side to the *Angiosporæ* by their germination, and on the other to the *Gymnosporæ* by the formation of their propagating cells. The sporocarps of the *Riccieæ* and *Blasiæ* might perhaps present some analogies with the sporocarps of the nucleolar Lichens. At the same time, however, the proembryo, by its different modes of development into a plant, furnishes us with a ground of separation into two distinct groups. In the schematic ambiguity of the word "*root*," which we find in the place of a clear idea among most botanists, it has escaped them that Mosses and Liverworts have no analogue of a *root*, and that the bud rising from the Conferva-like tissue of the proembryo, only morphologically limited in an upward direction, developes itself into definite forms, stems and leaves (fronds), while below it is lost in the Conferva-like threads of the proembryo, and is thence incapable of all further development in this direction in a morphologically distinct manner. We might say, with C. F. Wolff, that there is only one *punctum vegetationis* present here, whilst in the remainder two, an upper and a lower *punctum vegetationis*, manifest themselves, being divided by the intervening primary cells, which cause the course of development into two opposite directions, upward to the stem and downward to the root. On this account almost all perennial rootless *Agamæ* decay away below in proportion as they develope upwards, whilst the other kinds are developed in both directions and are thus able to increase in mass. A physiological difference corresponds remarkably with the morphological one mentioned.

* Compare H. Mohl, in the Flora of 1833, p. 33.

The rootless *Agamæ* agree so far with the *Gymnosporæ*, that they show no trace of a distribution of the fluid from a definite point through the plant, or even appear to admit of the possibility of such a thing. Indeed they do not need liquid water for the nutrition of all their separate parts, yet they require an atmosphere saturated with vapour. A plant of *Polytrichium*, for instance, with its lower extremity in water, and its surface protected from evaporation by oil, or exposed to a dry atmosphere in a state of agitation, will fade as far down as it is out of the water, and decay, but will vegetate vigorously again as soon as it is surrounded, by means of a glass bell, with an atmosphere saturated with aqueous vapour.

### a. *Rootless Agamæ.*

### IV. LIVERWORTS (Musci hepatici).

§ 97. The developed plant, like the Mosses, has no proper root. The stem manifests two main forms: first, the ordinary one, analogous to the stem of the Mosses; and secondly, another in which it is expanded into flat and more riband-like form, instead of in a linear direction. The former has always fronds (leaves), the latter, only the rudiments of such, or none at all. The former is seldom upright, but recumbent; the latter (*caulis frondosus*) is either partially developed in a filamentous form, and only flattened at the extremity, or wholly and entirely flat; in both cases it is differently formed, but most frequently forked or digitate, and very rarely pinnate. In a small number, for instance, *Riccia fluitans*, *Anthoceros lævis*, &c., the whole plant consists only of tolerably uniform flattened cells, ranged side by side, which can neither be considered as stem or frond. Here the bifurcated division predominates very considerably, and the manner in which the plants grow in all directions from one point gives the *Riccieæ* in part a great resemblance to Lichens. Fronds (leaves) occur in all Liverworts, at least as parts of the fructification, although in the case of the last-mentioned this is somewhat doubtful. The forms of the leaves are very various. With but few exceptions, the leaves are so directed that they lie in one plane on either side of the stem; on a flat stem they are very stunted, and occur upon the lower surface only. The leaves are occasionally cut into filiform segments, more rarely simple, frequently multifariously lobed at the margin, either bifid or multifid. In the bifid we often find a large and a smaller lobe (*auricula*), and the leaf folded together in the line of division between them. The stem has frequently two kinds of leaves; larger ones above, which appear to be in two lines on a depressed surface, and smaller ones varying in form, and which occur only upon the lower side of the stem (*amphigastria*, *stipulæ*). In the axils of the leaves, buds are developed, and from these ramifications which give not unfrequently a pinnate appearance to the stem, owing to the leaves expanding in one plane surface. Even in Liverworts, particular cells occasionally emancipate themselves from the general combination of individuality, and become developed into new plants; whilst in

connection with the plant they are converted into small cellular corpuscles, often surrounded by a peculiar crescentic cup-shaped or flask-like elevation of the upper cellular layer (*conceptaculum*), as, for instance, in the *Marchantia*.

Until a very recent period, Liverworts (with the exception of a few individual and unimportant researches) were merely objects of petty species-making. It is only in our own day that two men, Lindenberg * and Gottsche †, have zealously directed their minds to the subject; to the latter we are especially indebted for the interesting facts he has contributed concerning these beautiful plants. I cannot myself venture to say much on the subject, as I have not as yet had any opportunity of instituting very extended investigations into the nature of these plants.

More comprehensive investigations into the history of their development were first afforded us by Gottsche (*loc. cit.*), relative to *Jungermannia bicrenata*, *Preissia commutata*, *Blasia pusilla*, *Pellia epiphylla*, to which we may also add the observations of Mirbel on the *Marchantia polymorpha*. These acceptable contributions, however, still leave much to be desired, particularly in reference to the origin of the cells and the development of the leaves. From what has been published, we learn that the development of the spores exhibits no such sharply defined type as in the succeeding groups of the *Agamæ*, at least not such as in the Mosses and Ferns.

The forms unfolding themselves manifest as yet a very vague character. In the lower, leaves are wholly wanting; and here, consequently, the predominance of fancy over observation, which we so frequently meet with, has caused much to be said of the notion of the fusion of the leaves in the stem. As no leaves are present in the *Jungermannia multifida*, none are to be found, but in this case they are just as little fused into the stem as in *Melocactus* and *Euphorbia meloformis*. It does not at all follow that a plant must have leaves and a stem, but it is certainly purely in accordance with our experience to assume that some plants exhibit two essentially different processes of development, and that from these, two essentially different forms, as leaf and stem, may appear: where nature abides by only one of these processes of development, a stem without leaves will alone occur; and where the process is again different from this, neither stem nor leaf will be found. If we do not seek for definite conceptions of the history of the development of a plant by an inductive course, we may give free scope to our fancy, but we shall never learn to understand nature.

In the *Angiosporæ* we could not distinguish individual growth and individual repetition by gemmation, on account of the morphologically undefined character. Similar examples occur in the Liverworts in the ramification of the flat stem without any preceding formation of buds. In the Mosses no case of the kind occurs, as far as I know. In the Ferns and the *Rhizocarpeæ* a few instances present themselves; but not afterwards, unless we except the case of the *Podostemeæ*, with which we are still very imperfectly acquainted.

The forms of leaves appear only gradually in this group. In the

* Lindenberg, Ueber die Riccieen, Nov. Act. L. C. xviii.

† Gottsche, Anatomisch-Physiologische Untersuchungen über *Haplomitrium Hookeri*, Act. A. C. L. C. N. C., vol. xx. pt. i p. 207. At the present moment, unfortunately, another excellent set of observations by the same author are not yet in the hands of the public.

lowest they are entirely wanting; in the *Marchantiaceæ* they appear as small membranous narrow strips upon the lower side of the flat stem. In the *Jungermanniæ* the most frequent form is the bifid, folded together, and often associated with stunted leaves at the lower side of the recumbent stem. We still require more comprehensive observations of the history of the development of leaves than Gottsche (*loc. cit.*) has been as yet able to afford us. In the bifid leaves we must mention the peculiarity that in the smaller lobes, which are at first always flat, the cells sometimes increase only on the surface, and not at the margin, expanding in such a manner that the surface is inflated like a bladder, until finally the lobe of the leaf becomes hood-shaped.

I must refer to what is stated under the head of the Lichens and Mosses for the import of the particular cells of the parenchyma of the leaf and stem, which, regarded as peculiar organs (the so-called *gemmæ*, brutknospen), develope into independent plants. According to Bischoff (Bot. Termin.), both the cells of the stem (*Jungermannia bidentata*) and those of the leaves (*J. exsecta*) separate themselves as propagative cells (Brutzellen) from the plant, and isolated cells shoot out and develope while still connected with the parent plant into small cellular bodies (*J. violacea*), which separate from the plant, and grow into new plants, as in *Mnium androgynum* among the Mosses. The development of these structures had been thoroughly worked out by Mirbel in the case of *Marchantia polymorpha.*

§ 98. The organs of reproduction in Liverworts do not differ essentially from those of the Mosses; but the envelopes appear more clearly as special organs, or as more decidedly distinct from the other foliar organs.

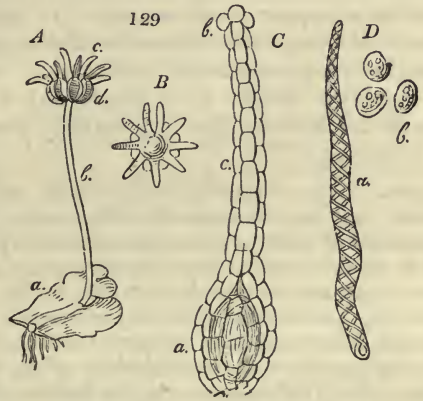
*A.* A definite number of leaves, differing more and more in form from the others, as we examine them from without inward (or upon the stem from below upwards), partly unconnected and partly growing together at their lower part, surround the organs serving for the formation of the spores, and thus compose a blossom (*flos*). Here we may frequently distinguish an inner circle of essentially different leaves generally grown together into a cup-like form, as constituting the perianth (*perianthium*). Between these and the origin of the fruit a peculiar cup-like organ (*calyx*, Gottsche) is often found, which is sometimes developed downwards in a remarkably unequal manner on the opposite sides, so that the peduncle of the fruit arises from the base of a hanging sac. In most Liverworts these blossoms are single; in many they are, however, grouped together in a definite manner upon a flat stem, and thus form an inflorescence (*inflorescentia*). In this we may distinguish the blossoms from the stalk supporting them, the peduncle (*rhachis*), on which the blossom always forms a small head. The end of the peduncle is sometimes simple, as in *Lunularia;* sometimes expanded in a knob-like form, *Grimaldia;* and sometimes either shield- or disc-shaped, when it is generally lobed, as in *Marchantia.*

We cannot speak specially of the formation of the blossom in the Liverworts, and of the calyx in its two forms (if indeed the two structures really have the same signification), until we have obtained those fuller

reports now in preparation by Gottsche on the history of their development. Bischoff* has furnished us with beautiful analyses, enriched by his admirable powers of delineation, but unaccompanied by any history of development, and constantly interspersed with inapplicable comparisons.

*B.* The blossoms enclose the first germs of the fruit (*germina*), intermixed with the so-called sap-filaments (Saftfäden, the *paraphyses*). They consist of an envelope (*calyptra*), and a nucleus; the upper end of the former is of variable length, directed upwards, and often terminates in a funnel-like expansion.

By way of illustration I subjoin a diagram of the germs of the fruit of *Marchantia polymorpha* (fig. 129.). Gottsche has made a step in ad-




vance of other observers in his investigations into the origin of the structure: according to him it seems certain that the nucleus becomes subsequently developed into the investment or case, but the "how" is by no means perfectly clear in this process. At first it appears to be a simple cell, which afterwards passes over into a small ovate body of cellular tissue.

*C.* On its further development, the envelope is gradually torn open, and the sporocarp, now becoming fully formed, emerges from it. In *Anthoceros* alone it appears raised like a little cap, from separating below the point. In the *Ricciea* it remains closed, as the nucleus does not become at all elongated in its formation. In the nucleus itself we can only distinguish two portions of cellular

* Bischoff, Bermerkungen über die Lebermoose, &c., in N. A. L. C. vol. xvii. pt. ii. p. 909. (1835).

129 *Marchantia polymorpha.* *A*, A part of the plant. *a*, Flat procumbent stem. *b*, Thinner erect part of the same. *c*, Lobed expansion of the stem, which bears upon its lower surface the sporocarps (*d*), surrounded by foliaceous organs. *B*, The lobed expansion of the stem bearing the sporocarps, seen from above: the slit in the two upper lobes corresponds to the attachment of the stem (*b*) of the former figure. *C* is the germen, fully developed. At *a* we see the nucleus already appears as one single large cell in the interior; at *c* is the so-called style; at *b* the so-called stigma. *D*: *a*, the so-called elar, from the ripe sporocarp; *b*, the spores.

tissue; a lower one, which, excepting in *Ricciea*, is elongated into a pedicle (*seta*); and an upper one, which becomes a spherical sporocarp (*sporocarpium*) in *Jungermannia pusilla*, and a filiform one in *Anthoceros*. The cellular tissue of this upper part is, again, very variously formed. The most external layers of cells become thickened, and form the wall of the sporocarp, which is afterwards torn up from above downward in various ways. In rare cases a portion of the central tissue remains under the form of a central columella, long in *Anthoceros*, or short as in *Pellia epiphylla*. Generally speaking, it is wholly converted into two different forms of cells: parent cells (in each of which four spores are formed and become clothed by a special membrane), which subsequently become absorbed, and elongated fusiform cells, containing from one to three spiral fibres, and which sometimes appear loose amongst the spores (*Fegatella conica*), sometimes adhering to the columella (*Pellia epiphylla*), sometimes on the margin (*Jungermannia bicuspidata*), or on the point (*J. pinguis*), or on the inner surface (*J. trichophylla*) of the valves; or in rare cases, as in the *Ricciea*, they are entirely absent. They are termed elaters (*elateres*).

The development of the originally homogeneous cellular tissue into such different kinds, that the homogeneous is torn away from the heterogeneous in consequence of their hygroscopic and elastic properties, occurs here as in the Moss capsule; and at any rate, during the present imperfect state of our knowledge, we have as little to do in the one case as the other with a separation into original separate parts merely grown together. The manner in which the separation of the parts is effected is very various; sometimes there only appears a cleft (*Monoclea*), or the wall is split more or less deeply into valves (*valvulæ*) varying in number from two to eight (*Pellia epiphylla*, *J. platyphylla*, *complanata*), or into many teeth (*dentes*), more rarely into irregular shreds (*Grimaldia hemisphærica*). In more rare cases a separation takes place around the fruit, so that the upper portion falls off as a cover, as in *Fimbriaria;* in the *Ricciea* it remains closed until destroyed by external agencies; in *Riccia* itself it is absorbed, so that the spores lie free in the cavity of the *calyptra*. More exact observations probably yet remain to be made concerning the development of the spores. I noticed that there were in the earliest stages always four spores free in the parent cell. I have not hitherto discovered any trace of a division of parent cell by the growing in of a partition wall, as Meyen describes*; but my observations are as yet very incomplete. We have some excellent remarks by Hugo Mohl† on the formation of the spores in *Anthoceros lævis*, which appears to correspond closely with the formation of the pollen.

*D.* The antheridia, whose forms and development entirely correspond with those of Mosses, consist of a pedicle, which varies in length, or is entirely wanting; and of the upper part, which is always spherical or ovate. The leaves rarely form special envelopes for these structures, although several leaves are frequently crowded more closely together at the end of the stem, concealing

* Meyen, Pflanzenphysiologie, iii. p. 391.
† Mohl, Linnea, vol. xiii. p. 273.

antheridia in their axils, and are then combined together as a catkin (*amentum*). In flat-stemmed Liverworts, the antheridia are always imbedded in a cavity in the substance of the stem, opening outward. In many we find them very much scattered upon the surface (*Pellia epiphylla*); in others a definite part of the stem, rising in a disc-like form, bears the antheridia (*Fegatella conica*); in others, again, this disc rises shield-like upon a pedicle, and is then frequently notched, lobed, &c., at the margin, as, for instance, in *Marchantia polymorpha.*

As I purpose saying what is necessary of the signification of these antheridia under the head of Mosses, I will here pass the subject by, merely giving *Fegatella conica* as an illustration (fig. 130.). I must, however, be permitted to remark that here, also, hasty observations have led to remarkable misconceptions. Almost all manuals speak of flask-shaped antheridia extending upwards into a long neck: none such, however, are to be met with. In *Marchantia polymorpha* and others, the cavity has a flask-like form, enclosing the antheridia below, but open as a narrow canal at the top, which sometimes rises cup-shaped above the surface of the stem, as in *Anthoceros*, as a papilla, in *Pellia epiphylla*, or as a pedicle, in *Riccia*. Within, this cavity is invested with a dense epidermis. On a superficial examination the flask-like outline of this epidermis has been mistaken for the antheridium, which is entirely separated from that membrane, lies under the canal, and is always rounded off at the end in an upward direction. In like manner the so-called *cuspides* in *Riccia* do not belong to the antheridia, but to the elevation of the parenchyma at the margin of the cavity enclosing these antheridia.

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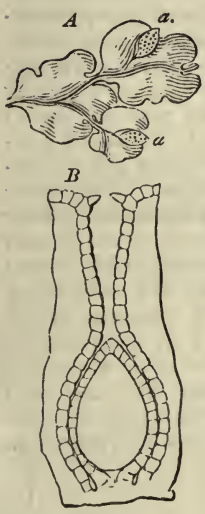


§ 99. The roundish stem of the Liverworts has a wholly similar composition to that of Mosses. The leaves, on the other hand, consist, without exception probably, of merely one simple cellular layer. The flat stem presents many varieties, consisting frequently of one simple layer of thin-walled cells, or it exhibits in its axis the elements of the ordinary stem. The parenchyma around this is formed of one or many cell-layers, often covered on the surface with a perfect epidermis, containing stomata of a peculiar kind, namely, wart-like, elevated cellular masses, perforated at the point by an intercellular passage, which leads into a cavity invested with lax and often flask-shaped cells. In *Fegatella* and *Marchantia* the cells of the central mass of the stem have beautifully porous or

[130] *Fegatella conica.* *A*, A portion of the little plant, with two disc-like elevations of the stem (*a*, *a*), in which the antheridia are imbedded. *B*, A part of a section of one of these elevations. The hollowing in is of a flask-like form, furnished with a tough epidermis. The antheridium consists internally of a cellular sac, filled by one large cell.

reticulated thickening layers. The pedicle of the sporocarp consists always, up to the period of maturity, of a delicate cellular tissue, which expands with wonderful rapidity, but at the same time also decays very quickly. The wall of the capsule consists, with few exceptions, of an epidermal layer (of flat and mostly brown-coloured cells), and of an inner layer of spiral-fibrous cells.

Liverworts deserve, in an anatomical point of view, much more thorough and comprehensive investigations than they have as yet met with. We most certainly possess the complete monography of *Marchantia polymorpha* furnished us by Mirbel, who has also given us plates which do more to dazzle by the brilliancy of their colouring than to satisfy, on all points, with respect to their fidelity to nature: but Mirbel leaves many questions unanswered, and his statements have already met with many corrections. Here, as everywhere else, we look in vain for an exact and complete history of the course of development. The formation of the spiral filaments in the elaters and the walls of the fruit have been observed by Meyen. According to his views, they arise from the perceptible confluence of the globules of chlorophyll into a spiral band. Gottsche positively denies this to be the case, and, as far as I have been able to convince myself in *Pellia epiphylla*, I think he is in the right. They differ in their fully developed condition from all other spiral filaments by their deep brownish yellow colour, which reminds us of the cells of the sheaths of the vascular bundles in the Ferns. A few special peculiarities present themselves in Liverworts; thus in the *Marchantiæ* we find air-cavities, in *Pellia epiphylla* a singular system of intercellular passages, which convey, not air, but a yellowish and, in the case of *Var. æruginosa*, a reddish juice.* Still more remarkable is the system of tubes discovered by Gottsche in *Preissia commutata*, running through the cells, and apparently perforating their walls: the only analogy with this case presents itself in the tubular convolutions of the root-cells of *Neottidium nidus avis* (vol. i. §. 39).

## V. MOSSES (Musci frondosi).

§ 100. The spore-cell expands, emerges from its torn outer coat, and, new cells being developed at the free end, forms for itself a filamentous tissue, composed of linear cylindrical cells ranged end to end (the *proembryo*). At one point, the filaments of this tissue become contracted into a node composed of closely compressed roundish cells; this node, elongating itself upwards, becomes the stem, on which leaves are simultaneously formed. More rarely the plant remains simple (as in the annual *Phascum*, and in the perennial *Polytrichum*), but there generally appear at the axils of the leaves small buds, by which means the stem ramifies. The form of the uniformly simple flattened leaves (which are never lobed) varies between almost circular, linear-lanceolate, and linear; they sometimes exhibit two streaks of denser, more compressed,

* Compare Wiegmann's Archiv, Jahrg. v. vol. i. p. 280. (1839).

and elongated cells (*nerves*) proceeding from the base, which sometimes stop at the middle of the leaf, and sometimes run along its whole length; in some, as in *Mnium punctatum*, we also find two marginal nerves. The leaves are simple, dentated or ciliated, generally scattered (spirally?) round the stem, sometimes apparently two-ranked, the stem with the leaves looking as if pressed flat (as in *Neckera crispa*, *Hypnum undulatum*, &c.). In some few Mosses the leaves actually do occur in two lines, and then differ very much from each other in their structure, as in *Fissidens*. Here the face of the leaf is folded together, and embraces the stem with the next leaf; above, however, it is continued in a simple, laterally flattened, uniform lamella (similar to the leaves of the Iris). In many Mosses the curved leaves are all bent at the point towards one side (*folia secunda*), as, for instance, in *Hypnum cupressinum*, *lycopodioides*, *scorpioides*, &c. On the first appearance of the stem, it exhibits, especially near the leaves, more or less numerous, longer or shorter filaments of cylindrical cells (adhering fibres, *rhizinæ*), which have been termed roots or root-fibres when they appear below, and sap-filaments (*paraphyses*) when they occur above, especially between the organs of propagation.

Our knowledge of the course of the development of Mosses, and of the morphological laws by which it is regulated, are still very defective; for instance, we are wholly unacquainted with the history of the development of the leaf, and consequently of the importance of its relation to the stem. We have as yet nothing more exact regarding the germination than what the observations of Hedwig* have given us, although there has been no lack of fantastic specious theories. When I find a description of moss germination beginning thus—" Soon after the escape of the seed *there unfold themselves, as it appears* from the *solution* of several decaying germ-granules," &c. — I lose all further desire to continue the perusal. Here we may see at once that the author cared less to give a certain and clear exposition of a strictly scientific observation, than to expatiate in an assumed ingenious manner upon incomplete and superficial views. A fundamental repetition of these investigations is earnestly to be desired; and until this has been made, that is, until the morphological relation existing between leaf and stem has been clearly ascertained from the history of development, nothing definite can be said concerning the morphology of Mosses. A short notice of the mere facts is given in the paragraph. The proembryo has been already described as *Conferva castanea* Dillw, and as *Catoptridium smaragdinum*, in *Schistostega osmundacea*. According to more recent views, the Moss has been regarded as formed of *Confervæ* grown together, under the impression that such a confusion of ideas would make the matter more comprehensible.

Thus much is at any rate apparent from the history of germination, that we cannot speak here of a root as morphologically opposed

* Hedwig, Fundamenta Hist. Nat. Musc. Frond, Leipzig, 1782.; Theoria Generationis et Fructificationis Plant. Crypt., Leipzig, 1798. I have unfortunately not become acquainted with the very recent work of Bruch and Schimper, and consequently I do not know whether it contains anything more.

to the stem. On isolating a young plant of *Funaria hygrometrica* (fig. 131.), it will appear to be merged below into the *Conferva*-like cells of the proembryo (*b*, *b*), or rather grown into it, and only separated with morphological distinctness in an upward direction (*a*). This justifies the definition of frondose Mosses as rootless *Agamæ*. My investigations into the development of the leaf, which are unfortunately still very imperfect, show with certainty, at least in *Sphagnum*, that the leaf as in the *Phanerogamia* is protruded from the axis, and that, consequently, the idea of a leaf and stem, as I define them, may be fully applied to Mosses. The stalks often range themselves irregularly, especially in the upright stem (here they are sometimes pyramidal), but likewise in the recumbent and floating stem; they are more rarely (apparently) pinnate (as, for instance, even in *Hypnum molluscum* and *Crista castrensis* &c.) in most stems pressed to the ground. The condition of the highly hygroscopic leaves, when perfectly dry, is also peculiar and important with respect to the determination of species, as they curl up in a very definite and diversified manner (as, for instance, in *Orthotrichum crispum*). In Mosses growing in the water, the central nerve remains frequently upon the stem, as a little point (*caulis spinulosus*, in *Fontinalis*) after the destruction of the substance of the lamina. In some Mosses small lamellæ are found, placed lengthwise, either upon the central nerves (*Catharinea*) (fig. 132.), (*Schistidium*), or upon the whole surface of the leaf (*Polytrichum*). We but rarely find different leaves upon the same Moss, as in *Sphagnum*. Here the lateral stalks are collected in little bundles, two generally hanging down, while the others stand straight out: these latter have always differently formed, narrower leaves than the former, and both generally deviate regularly in their form from the stem leaves. Occasionally the leaves first originating in germination differ from those subsequently formed upon the full-grown plant

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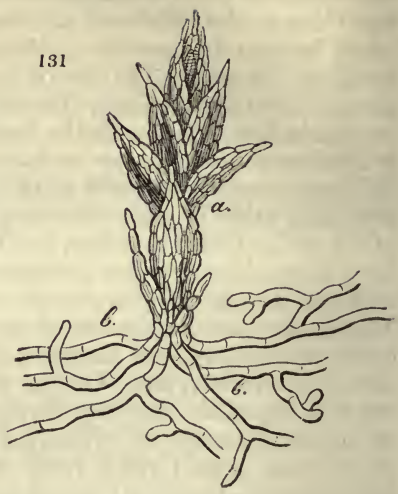


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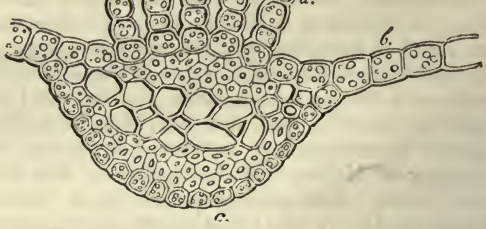


[131] *Funaria hygrometrica.* The little plant (*a*) has arisen in such a manner from the filaments of the proembryo (*b b*), that no distinctly marked radical extremity is to be defined below, the plant passing gradually into the filiform cells of the proembryo.

[132] Section through middle of leaf of *Catharinea undulata.* Upon the central nerves (*c*) are lamellæ, placed lengthwise (*a*); at *b*, leaf-cells. The central nerve consists of much thickened, liber-like cells, and other larger thinner-walled cells enclosed by it.

(into which their forms, however, gradually merge) (fig. 131.). The adhering fibres are also at times developed from the leaf-cells, as, for instance, in *Calymperes*, *Syrrhopodon*, &c., and are regarded here as parasitical *Confervæ;* a view that is evidently devoid of reason, since the immediate development of individual leaf-cells into filiform cells is generally the first beginning of their formation.

There are many examples in this group of separate cells of the stem (*Mnium androgynum*), as well as of the leaves (*Syrrhopodon prolifer*), severing themselves from the connection of individuality of the whole plant, and introducing an independent process of cell-formation, from which a little cellular body proceeds, emancipates itself from the plant and develops into a new cell. These have been named proliferous buds (*gemmæ proliferæ, bulbilli*). They are neither buds nor bulbs, if we connect definite conceptions with these words, and not something defined in opposition to all laws of the formation of ideas, as "A bud is that body from which a new plant may proceed, and which is neither a spore nor seed." Investigations on the development of these cells are, however, still incomplete; we are indebted to Meyen* (*Mnium androgynum*) for the best we possess, and from his statements it appears certain that a single cell of the extremity of the stem becomes the base of the new individual.

§ 102. *A.* Sometimes terminal, sometimes lateral, closed buds, composed of many, most frequently narrower and differently formed leaves, and many somewhat irregular adhering fibres (sap-filaments, *paraphyses*) which often occur in the interior of the bud, may, as the special coverings of certain organs, destined to develop themselves into the sporocarp, be comprised under the term of *blossoms* (*flores*).

It appears to me, in a twofold point of view, to be purely sporting with the subject to regard the blossoms of Mosses as essentially monosexual, and naturally collected into an inflorescence, merely for the sake of dividing, without any reason whatever (but purely in accordance with wholly arbitrary and inapplicable analogies with the higher plants), that which nature exhibits to us as a wholly independent structure, in order ingeniously to put it together again. In our present knowledge of the blossoms of the Mosses, there is at any rate no indication that any definite parts within it are more closely combined by nature, and, consequently, nothing that can give probability to the view of the composition of the whole blossom from separate florets. Here, as everywhere else, I strictly abide by that which nature actually yields. Secondly, the opinion that all the blossoms of Mosses are essentially of one sex is untenable, because, at the present time at least, there can be nothing said of sex with reference to Mosses; notwithstanding that the pistillidia and the antheridia may be situated upon different plants, as, for instance, in *Funaria hygrometrica* (fig. 133. *a*), it

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* Meyen, Wiegmann's Archiv, Jahrg. iii. vol. i. p. 424. 1837.

[133] *Funaria hygrometrica:* two young plants. *a*, With the sporocarp (still enclosed by the calyptra (*c*), and very young) in the act of development, and *b* bearing anthers.

being in the present day mere fiction to ascribe any sexual signification to the latter. Besides this, the floral leaves are by no means distinctly different from the true leaves, into which they generally pass by imperceptible gradations, and there is no appearance of the formation of a calyx, which would, indeed, constitute the most essential morphological distinction between the Mosses and Liverworts. Even for this reason, it is impracticable to distinguish the separate blossoms and the inflorescence in the Mosses.

*B.* The primary form of the sporocarp, the archegonium (*germen*), is that of a shorter or longer ellipsoidal, attenuated corpuscle, stalked at the base. It consists merely of a simple layer of cells, the envelope (*calyptra*), which extends upwards into a longer or shorter filament, expanded somewhat funnel-like at the extremity, and enclosing a nucleus free at all parts except the base. This conceals, under a simple epithelium, a delicate walled, uniform, cellular tissue, capable of development.

The archegonium of Mosses is so strikingly similar to that of the Liverworts, that whatever may be said of the one, applies also to the other. We stand, unfortunately, in the midst of such uncertainty here, that all our attempts at a morphological explanation of what follows, even where they may not be purely visionary, are still wholly unstable; so it is certainly not worth while to attempt going beyond the point to which the bare fact may lead us. How has the *archegonium* originated? Is the separation into *nucleus* and *calyptra* original, or been produced subsequently from continuous cellular tissue? Has the *nucleus* or *calyptra* been first formed? In what relation do both parts stand to leaf and stem, &c.? These are questions which must be answered, by means of a previously and carefully pursued history of development, before we can entertain a remote hope of arriving at a scientific comprehension of the capsule of Mosses. It will, of course, appear most evident, that designations such as *style* and *stigma* for the filiform extremity of the *calyptra* must be alike unmeaning and false, since they designate organs of the *Phanerogamia* defined according to morphological and physiological characteristics. The inner cellular tissue of the *nucleus* consists in the earliest conditions that have, as yet, been observed, of but a few cells (often of no more than some twenty in the cross-section). From this tissue are developed the operculum, the peristoma, the wall of the capsule, the columella and the speedily disappearing sporangia, and, finally, the spores; from which we may satisfactorily see the falseness of the expression *massa sporigena*, as applied to this cell-tissue.* Concerning the filiform end of the *calyptra*, the inappropriately termed *stylus*, there is still much doubt, whether it is a canal, or a solid mass; and, if the former, whether it is hollow from the beginning, or only developed by subsequent expansion into a canal. All this can only be decided with certainty by the history of development. It is certainly in favour of the opinion of the original difference of the capsule and the nucleus, that a decided integument is subsequently developed upon the sporocarp formed from the nucleus, since, as yet, at any rate, we are unacquainted with any instance of a cellular layer, originally connected with other cells,

* We might just as well term the yolk of the egg *massa pterygogena*, because birds, amongst other things, have also feathers.

being converted into an epidermal layer. When Bischoff * maintained that the term *epidermis*, used by Mohl, is inapplicable here, owing to its being at variance with the morphological signification, I know not what he can mean, since, as we have just shown, we know nothing about the morphological signification of a sporocarp. On the other hand, the simple cellular structure of the nucleus renders it in the highest degree probable that it is only a simple organ, and that all the various regions that appear in the sporocarp originate by internal separation (which is partially of a purely mechanical nature), and are all parts produced from one and the same mass of tissue, and from one and the same organ; at all events the idea of the capsule being formed from the growing together of as many leaves as the peristoma shows dentations, as maintained by many (Bischoff † among others), is a most perverted one. For, as has already been remarked, the whole section of the nucleus (which, besides the dentations, must also form the columella and the spores) has in its early condition fewer cells than there are subsequently teeth; and, however moderate we may be in our claims, we must demand at least one cell for each leaf in its first deposition, setting aside that, as far as the structure of the inner peristoma is concerned, the whole thing is devoid of sense, and that the assertion must fall to the ground, being a mere fiction. ‡

*C.* In the development of the archegonium, the *calyptra* is torn off at the base, and remains, for a longer or shorter period, thus hanging to the sporocarp, by the expansion of which it is sometimes also laterally split. A small piece of the *calyptra* always remains at the base, and this, in connection with the somewhat developed point of the stem, forms a small sheath (*vaginula*) around the base of the sporocarp. In the nucleus we may distinguish, (*a*) an upper, (*b*) a middlle, and (*c*) a lower mass of cellular tissue, which are variously developed at *a* to the *seta*, at *b* to the *theca*, and at *c* to the *operculum* and *peristoma*.

* Bischoff, Handbuch der Terminologie, p. 687, Bemerk. 33.

† Bischoff, Handbuch der Botanik, vol. i. p. 430.

‡ That even such sensible men and excellent observers as Bischoff should give themselves up to this childish sporting with comparisons, must be wholly inconceivable to those who have not studied the history of modern philosophy since Kant, and become acquainted with the injurious influence exercised upon the development of our scientific progress by the apparently intellectual sense, but actually mere shallow twaddle, which Schelling gave forth as natural philosophy. (See the work of Fries, entitled Reinhold, Fichte, and Schelling, Leipzig, 1803.) A few hollow set phrases, endowed with such an unmeaning power of generalisation that they were alike applicable to all subjects, and garnished with the trivial comparisons of superficial wit, which is far more common than scientific acuteness, sufficed to lull the great mass of those who would willingly *know*, without having the trouble of learning, into the pleasant delusion that they had actually seized science by the forelock. Even in science, unfortunately, numbers give strength; and he who understands how to throw dust in people's eyes, will, at least for a time, be regarded with consideration; and he who may be hindered, by devotion to one special branch of science, from working out the philosophical groundwork for himself, will find it difficult, if not impossible, to remove himself from the general intoxication of a philosophical mania of the day. Thus, uncommon minds have been estranged from an earnest and strictly scientific research of nature, and, suffering their activity to be fettered by prevalent prejudices, have been lost to what is purely philosophical and scientific, and wasted their best energies in the visionary dreams of an unbridled fancy.

*a.* The lower cellular tissue is very much elongated, and thus forms a filiform support for the rest; sometimes it becomes blended with the middle one by a gradual swelling, forming the neck or *collum*, or it forms a more sharply defined thickening of a different form, the *apophysis*, especially marked in *Splachnum*.

*b.* The middle portion forms an urn-shaped, almost cylindrical, seldom obtusely angular, or plano-convex organ, and becomes developed into different layers: (1.) to a central, either cylindrical or more spherical, cellular mass, the *columella;* (2.) to the coating of the *theea;* and (3.) to a delicate cellular tissue lying between the other two, the cells of which, developing as *sporangia* into four (?) spores, become dissolved and absorbed, so that the spores are left free. Each spore-cell secretes within the sporangium a peculiar membrane, which is either smooth, or covered with larger or smaller warts and areolæ. The wall of the theca itself consists, externally, of an integument in which several layers of a thin-walled, close cellular tissue are formed — the outer membrane (*membrana externa*), internally of several layers of close cellular tissue — the inner membrane (*membrana interna*), surrounding the spores. Between these two lies a layer of extremely porous, often almost filamentous, loose cellular tissue, which is sometimes absorbed by the time the sporocarp is ripe.

*c.* The upper portion of the cellular tissue of the nucleus is developed into such heterogeneous cellular structures, that it separates, in drying, into many parts, by the unequal contraction, and the rending of homogeneous from heterogeneous rows of cells, partly from within outward, and partly in a lateral direction. A layer of more solid cellular tissue, in the form of a cover (*operculum*), either flattish, convex, pointed or peaked, separates on the exterior from the upper portion of the nucleus, and, at the same time, from the theca. In most Mosses an annular layer of three or four rows of cells (*annulus*) occurs, obliquely interposed from below and from without, upwards and inwards, between the theca and the operculum. In the interior, the columella is naturally continued from the theca into the point of the operculum. Its extremity appears sometimes on the falling off of the operculum, as a disc or membrane, closing the whole aperture of the theca (*stoma*). The remaining cellular tissue, between the end of the columella and the operculum, is developed into a highly hygroscopic tissue, which separates in various ways, either only laterally, into from four to sixty-four acutely pointed lobes, teeth (*dentes*); or, at the same time, from within outward, so that two rows of such lobules appear, the innermost of which, where broader and alternating with the teeth, are called *processes*, and the narrower ones occurring between these processes, the *cilia*. The inner layer occasionally appears to cohere, entirely or partially, into a membrane; but the external one more rarely. The cells of the external lobules, almost all manifest the peculiarity that their lower and upper walls become so

disproportionally thickened, that the horizontal partitions formed, by the drying of the cells, project laterally, as well as towards the interior and exterior, and are then designated *trabeculæ*. The inner lobules, when they are connected together as a membrane, are always merely the remains of torn cells.

I have here given the history of the development of the archegonium from confessedly proportionably circumscribed and incomplete observations of my own. By way of illustrating the terms applied to the individual parts of the ripe capsule, I here give the analysis of the sporocarp of *Hypnum abietinum* (fig. 134.) My investigations, combined with what

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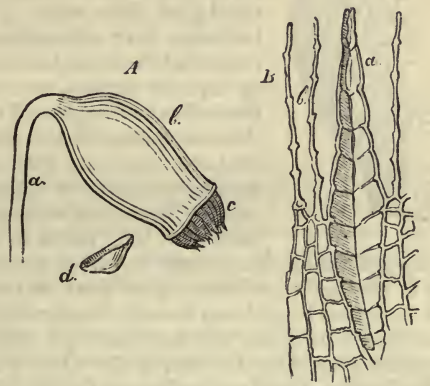
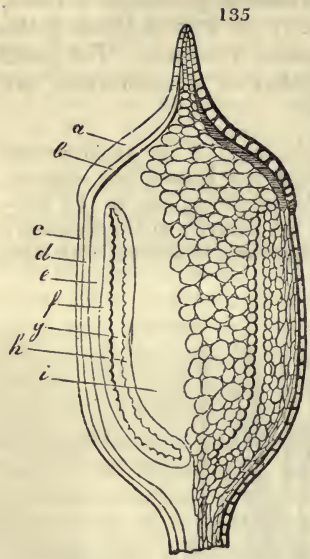



has here and there been contributed by others *, may perhaps suffice to confirm the representation given. It is very evident that there are still great deficiences to be lamented, and that innumerable questions present themselves, especially as to the manner in which separate cells and masses of tissues have originated. What appears from the facts with which we are already acquainted is, that so far as the history of the formation is known to us, a rending of a continuous mass of cellular tissue, but nowhere a blending together of divided parts, is apparent, and consequently that it is as yet, scientifically speaking, incorrect to regard the Moss capsule as grown together from different pieces. The very simple structure of the archegonium makes it certainly in the highest degree improbable that it will ever be found to be grown together out of different parts. The second point to be observed here is, that the archegonium consists of continuous cellular tissue from within outward, and consequently that the development into layers of different cells need not

* Especially H. Mohl, on the Spores of the Cryptogamia, Flora, 1838, vol. i. p. 33.; History of Development of the Capsule and Spore of *Œdipodium Griffithianum*, &c., by W. Valentine, Ann. of Nat. Hist., Aug. 1839, p. 456, &c.

134 *Hypnum abietinum*. *A*, The upper part of the seta (*a*), with the theca (*b*), the peristoma (*c*), and the operculum (*d*). *B* is a part of the inner peristoma, with processes (*a*), and cilia (*b*).




necessarily extend throughout the whole length. It is mere prejudice to regard the external peristoma as appertaining to the external, and the inner peristoma as appertaining to the inner, membrane. The anatomy of most Moss capsules near a state of maturity* shows evidently that the peristoma and walls of the theca do not stand in any nearer relation to each other than as cells to the parts of a plant generally. This may be plainly seen, for instance, in the section, cut lengthwise, of an unripe capsule of *Grimmia apocarpa* (fig. 135.). Starting from a one-sided and false view of the ripe fruit, botanists have accustomed themselves to regard all these anatomical individualities as especial organs, and then to seek for methodical arrangement for them; whilst the true mode of observation shows us that we have to do here with merely tolerably regular remnants of a torn organ. If, instead of inventing supposititious theories, pains had been taken to carry out investigations with somewhat more exactitude, it would soon have been discovered, at least in the inner peristoma, that there was no room here for many of the very ludicrous hypotheses broached regarding the subject. In the peristoma we must distinguish whether the third upper portion of the archegonium occupies a considerable part of the whole length, so that the peristomæ may be developed into vertical rows of cells, as in most cases, or whether, as in the *Polytrichoideæ*, &c., it is merely the flat upper portion of the theca, and is therefore rather a development in horizontal layers. Here, then, the inner peristoma or the membranous expansion of the columella are the same thing, and formed from one layer of cellular tissue. In others, on the contrary, a simple (?) layer is developed into the inner peristoma, directed inward from the wall of the operculum; on this first layer another follows, directed inward, the cells of which on a section all, or the alternate ones, resemble acute equilateral triangles, the bases of which are directed alternately outward or inward. In these cells the horizontal and the lateral vertical partitions become especially thickened, while the external and internal walls, on the contrary, become blended with the superjacent cells, and then separate subsequently from the other walls: thus the plaited membrane in *Buxbaumia*, *Diphyscium*, &c. is formed with some degree of regularity. If, on the other hand, cells that on a section appear uniform alternate with others (*Hypnum abietinum*, figs. 134. 136.), the persistent lateral partitions of the former

* Compare the remarkably beautiful delineations of H. Mohl, *loc. cit.*

135 *Grimmia apocarpa.* Section, lengthwise, through an unripe sporocarp. The cells are only marked upon the right side. *a*, The operculum; *b*, the teeth of the simple peristoma; *c*, the epidermis; *d*, the external, *e*, the middle layer of the wall of the theca, the former consisting of elongated, and the latter of very loose, cells; *f*, the innermost layer of the wall of the theca, bounding the space (*g*) in which lie the spores; *h*, external layer of the columella, likewise bounding the spore cavity; *i*, the cellular tissue of the columella, tolerably loose.

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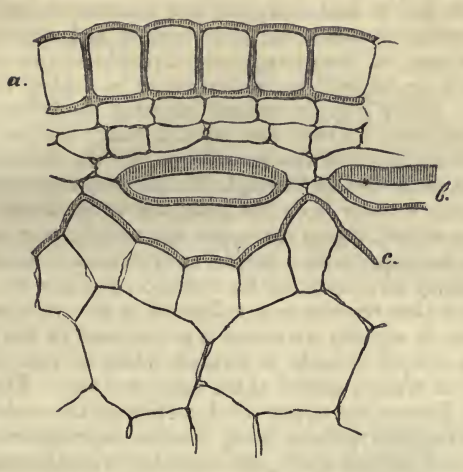


constitute the processes, and those of the latter the *cilia*, as, for instance, in *Hypnum*, and *Bryum*. A perfect, closed cell never, however, concurs in forming the folded membrane, nor the processes and *cilia* (so far as they are free from the interior outward). A wider field for more comprehensive and exact observations is opened here than I have hitherto been enabled to pursue.

I must not omit to mention a view which was first proposed by the acute Robert Brown*, namely, that in most peristomæes* the regular number of the teeth was 32, and that when fewer were present it must be considered owing to a growing together of several into one. At first sight this view presents much in its favour. But the circumstance that this law is not applicable to Mosses, the *peristomium* of which exhibits a greater number of teeth, is at once suspicious; besides, the history of development of the capsule of the Moss shows, as far as our knowledge of the subject extends, that we cannot speak of growing together in this case, but merely of more or less regular splitting down. Finally, regularity of number in teeth is by no means so firmly established as many might assume, for we not unfrequently find peristomæ in which there is one tooth too little, especially in the Mosses where the number of the dentations exceeds 32. The *almost* regular divisibility of the number of teeth by four must, however, always strike us as remarkable. The reason of this appears to be based upon the nature of the vegetable cell, and is thus determined with reference to teeth from their first formation. A comparison of the multiplication of cells in some of the *Algæ*, as, for instance, in Meyen's *Tetraspora*, with the almost constant formation of four spores and pollen-granules in one parent cell, together with

* Robert Brown's Miscellaneous Writings. (Germ. Trans. II. 734.)

136 *Hypnum abietinum.* Cross-section of the still green sporocarp, in the region where the cilia and processes are connected at the base. *a*, A deposit of thickened cells forming the operculum; *b*, separate cells, forming the dentation of the exterior peristomia; *c*, thickened walls, formed by a row of cells constituting the cilia and processes; the latter consist of parts which project externally, in the form of a Gothic arch.

a few other facts, appears to offer an indication of a parent cell always giving origin to two or four new cells, and that consequently in a limited but uninterrupted formation, the cells formed and the equally definite groups of cells must be almost regularly divisible by two or four. There is certainly nothing beyond an indication to be looked for here, and it would be mere empty play to attempt erecting an influential law upon so frail a foundation. There are, besides, many deviations to be met with in the development of the sporocarp. In the *Sphagnum* the protruding archegonium breaks through the calyptra in an upward direction instead of tearing it away from the base, but it does not form any long *seta*. In the so-called *Astomi* the upper and middle part of the archegonium becomes developed into a simple, entirely closed capsule, only subsequently irregularly torn open, as, for instance, in *Phascum*. The amount of cellular tissue that remains as a columella is also very variable, so that sometimes there is scarcely a trace of it to be found in the ripe sporocarp. In *Andreæa* a simple capsule is formed, which is rent lengthwise into four lobes, which remain united at the apex and base. Finally, in a great number of the Mosses the upper third portion of the archegonium forms merely the operculum, without being further heterogeneously developed inward: all these, consequently, are devoid of a peristoma. Meyen pretends to have seen spores formed in *Sphagnum* at the end of a cellular filament by the spontaneous separation of a parent spore, as in Liverworts. I have never been able to find these filaments, but I have easily succeeded in pressing out four perfectly free spores in a young condition from the parent cell (sporangium) in which they were enclosed. Finally, we meet with a deviation in some *Polytrichoideæ*, where four plates of dense cellular tissue remain between the inner membrane of the theca and the columella, dividing, until the sporocarp is nearly mature, the space destined for the spores into four parts. Many other interesting particulars may be found on this subject in Robert Brown's works * ; we have also recently obtained very excellent contributions on the development of the spores by Lantzius-Beninga. † The most important result of the latter work is the fact that the layer of the archegonium, from which the spores are subsequently developed, consists originally only of a single layer of cells, which are parent cells. Meyen says (in his Physiologie, vol. iii. p. 387.), "Robert Brown appears to have been of the opinion that the spores of Mosses are formed in the cells of the columella." Palisot de Beauvois had asserted that the true spores were formed in the *columella*, and that the loose granules deposited around it were the pollen. Robert Brown's assertions are directed against this false view, which he fully sets aside in his usual sure and profound manner.

*D.* Little buds similar to those mentioned at *A*, or disc-shaped as in *Polytrichum*, *Splachnum*, contain another peculiar organ (*antheridium*), which, as in the above mentioned, also occurs with archegonia even in the same blossom. The earliest condition in which it has as yet been observed exhibits a small ellipsoidal, longer or shorter pedicled, cellular corpuscle, having a dark opaque spot in the interior. Somewhat later, we may definitely distinguish a simple layer of cells, enclosing a large central cell, filled with turbid formative matter. Here we subsequently find cytoblasts,

* See R. Brown's Miscellaneous Works (*loc. cit.* II. 682—744.).

† De Evolutione Sporidiorum in Capsulis Muscorum. Göttingen, 1844.

and the whole central cell is finally filled with a close and very thin-walled cellular tissue. In each cell a spiral fibre of two or three coils is then developed. On their complete development the spiral fibres lie free in their cell, and manifest *under water* a rapid motion round their axes, which the free spiral fibres retain for a time after the destruction of the cell, and thus move onward in the water. In plants of the previous year we still find this organ, dried and shrivelled together, and, as it appears, deprived of its contents by an orifice in its upper part.

By way of illustration I give here the antheridia of *Funaria hygrometrica* (fig. 137 *b*, and 138.). With the exception of a few unim-

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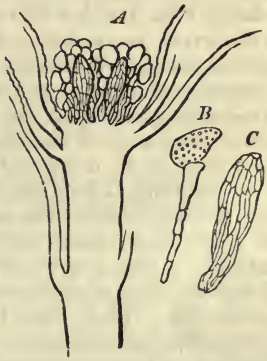


portant particulars, what is now given is all that we know of this organ, from which has originated so much confusion of ideas in science. Thus much appears fully certain, that neither in the history of their development, nor in their structure, nor in their physiological relation, do they show the most remote analogy with the anthers* of the *Phanerogamia*, and, consequently, that the application of this designation, together with all the visionary matter (the pretended theories) based upon it, are altogether devoid of all foundation, and therefore do not belong to science. So far as I know, no observer has as yet spoken of the central cell, which

* Although it is in the highest degree erroneous to name these and similar structures in the Liverworts anthers, yet, as they merit some peculiar designation, I retain this expression, however inappropriate it may be, which has already been so generally used, in order not to add to the confused nonsense that already characterises our terminology. I would expressly remark here, as I have done elsewhere, that the etymology has *no influence whatever* upon the determination of an idea, this being solely effected, in regard to a technical expression, by a scientific definition. A technical term is merely a sign easily conveyed by speech and in writing, which would have *no sense* were it not interpreted according to the definition applied to it in this one particular science. The best terms are always those whose etymological signification stands in no relation to the

[137] *Funaria hygrometrica:* two young plants. *a*, With the sporocarp unfolding (still enclosed by the calyptra (*c*), and very young (*b*) ), bearing antheridia.

[138] A long section through a so-called male plant of *Funaria hygrometrica* (*b* of the fig. 137.). *A*, On the apex of the stem are the antheridia (*C*), surrounded by paraphyses (*B*).

is so essential to the signification of the whole, and is so easily recognised, as in the case of *Sphagnum*, where it may with the greatest ease be isolated long before the origin of the cellular tissue. In like manner, the delicate cellular tissue which necessarily precedes the formation of the spiral fibres, and, according to my views, is far more essential than the latter, has been treated as a secondary matter by most observers, owing to the prejudice they had once adopted of considering the whole organ as a pollen-vesicle, and the contents as the matter of fructification (*fovilla*); entangling themselves in confusion in spite of their own senses. The spiral fibres have elicited the most observation, owing to the motion they manifest; and they have thus been elevated to the rank of spermatic animalculæ. In the course of my own careful examinations of *Polytrichum*, I have never been able to discover this motion when no water was applied upon the object-stage. When water was present, the fibres exhibited a rapid motion about the axis of the spiral, on which the fibre freed from the cell naturally assumed a progressive motion, in accordance with the law of the archimedean screw; I have never, like other observers, succeeded in detecting another motion, as, for instance, a change of the convolutions. As far as the form is concerned, I found fibres which had a spherical head at one extremity, or an elongated swelling gradually merging in the fibre, or a spherical protruberance below the other extremity of the fibre, or finally a spherical head with, some distance from it, an elongated swelling and, further below again, another spherical swelling. I hold all these forms, of which the last-named were of the least frequent occurrence, as mere unimportant irregularities occasioned by the adhesion of mucus, and not to be the heads of supposed spermatic animalculæ. I have also observed, where a simple head was present, that there was as often a progressive motion with the pointed end forward as the reverse. (See Plate II. figs. 9. and 10., with the explanation). The circumstantial description of the views of those who suppose that they have here found spermatic animalculæ may be met with in Meyen *, where the discrepancies occurring in the observations of others are remarked upon.

I will venture upon a supposition regarding the morphological signification of these parts when I speak of the ovule of *Phanerogamia;* of their physiological importance we know as yet nothing.

§ 103. The structure of Mosses also is still very simple. The stem exhibits in most cases a closed circle of elongated cells, some narrower and very thick-walled, others wider and thin-walled (circle of vascular bundles), separating the enclosed parenchymatous mass (*medulla*) from the outer portion (*cortex*). The leaves mostly consist of a simple layer of tabular parenchymatous cells, which have the lateral walls frequently porous, as *Dicranum.* The upper and lower walls not unfrequently exhibit a papillose projecting thickening, as in *Orthotrichum crispum.* The nerve consists either only of a few layers of somewhat more elongated cells, or of two bundles of elongated thick-walled cells, which arrange

subject, and which in the present advancing state of science, may thus place us beyond the reach of all the philological dilettante, with their ostensibly scientific remodelling of technical terms, and necessarily resulting increased uncertainty and diffuseness of terminology.

* Meyen, Physiologie, vol. iii. p. 208.

themselves above and below on the leaf-cells; or, finally, it is composed of an actual vascular bundle, that is, a large bundle of the above-described (liber?) cells, enclosing elongated wide thin-walled cells (vessels), which are either interposed between the two halves of the leaf, consisting of a single layer, as in *Catharinea*, or received between the two layers forming the leaf as in *Polytrichum*. The *seta* consists of similar elements to the stem, only that here the cells are generally thinner and longer. The cortical cells of the seta, the epidermal cells of the *theca* and of the operculum, the cells of the peristoma, as well as frequently the cells of the adhering fibres, have the cell-walls varying in colour from a light to a dark brownish yellow. The cells of the peristoma generally exhibit irregular wart-like thickenings upon their walls, which often appear so prominent, that in the case of *Bryum cæspititium*, for instance, the points of the dentations seem to be narrowly and deeply notched at the sides.

It is further remarkable, that the epidermis appears most perfectly developed on the collum and the apophysis, exhibiting stomates here. There is generally also a small quantity of loose spongy cellular tissue beneath it.

Simple as the structure of Mosses is, we are very deficient in exact observations regarding many particulars.* Thus the little stem of *Buxbaumia aphylla* exhibits much that is interesting, as, for instance, the indication of a reticular thickening of the cell-wall in the medulla. The leaves of Mosses and their nerves, also merit more thorough investigation than they have hitherto received. In *Catharinea undulata* (fig. 139.) the leaf, as in most other Mosses, with the exception of the species of *Polytrichum*, consists only of one layer of cells (*b*). The central nerve (*c*), however, which supports the affixed *lamellæ* (*a*), consists of an upper and lower epidermis, between which a true vascular bundle is interposed. This (see fig. 140.) consists of liber-cells (*b d*), enclosing between them

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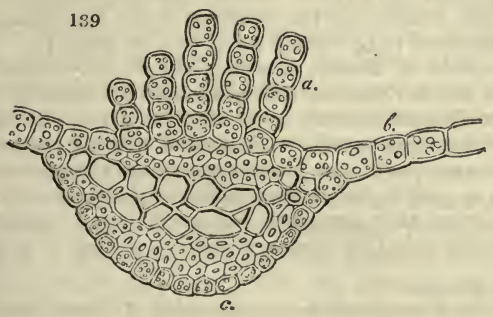


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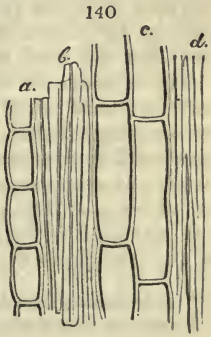


* Structure of the Seta in *Funaria hygrometrica*, by E. Lankester, in Ann. of Nat. Hist., by Jardine, Hooker, and Taylor, Feb. 1840, p 361.

[139] Section through the central part of a leaf of *Catharinea undulata*. *a*, On the mid-nerve (*c*) are erect longitudinal lamellæ; *b*, leaf-cells. The mid-nerve consists of very much thickened liber-like cells, and thin-walled wider ones enclosed by it.

[140] *Catharinea undulata*. Section, lengthwise, through the mid-nerve of the leaf.

long, very much expanded, cylindrical cells (*c*) (vessels in the simplest form). Robert Brown made the correct observation that in *Catharinea* the lamellæ are only inserted upon the mid-nerve, while in *Polytrichum* they are found upon the whole surface of the leaf. (See his Miscellaneous Writings.) It does not seem to me that Treviranus (in Linnæa, vol. xv. p. 3. plate 3. fig. 6.) refutes this view, or establishes his own that the whole is to be regarded as a nerve in *Polytrichum.* The lamellæ placed upon the surface of the leaf in *Polytrichum* exhibit the peculiarity that the lower cells are always thin-walled, while the upper and lateral especially are very much thickened. In *P. yuccæfolium* these upper walls are bent in, so that each lamella shows a furrow upon its free edge.

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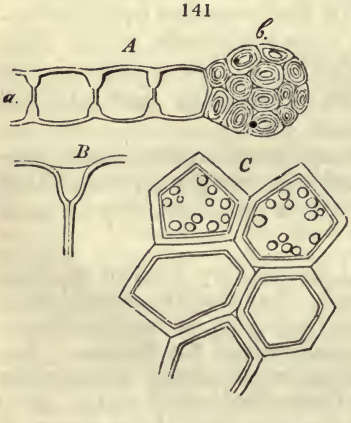


Many have contested the view of there being marginal nerves in the leaves of Mosses, but without having examined the subject. In *Mnium punctatum*, for instance, they are strikingly evident, and formed from thickened cells ranged in layers (fig. 141. *A b*). The cells of the lamina of the leaf (*a*) in this plant likewise exhibit interesting peculiarities from the manner in which they are ranged together, as may be seen from fig. 141. *B, C*). In a group* of Mosses consisting of *Sphagnum, Octoblepharum, Leucobryum, Dicranum glaucum,* and *Weissia verticillata?* the leaf is essentially composed of two different kinds of cells; namely, some that are closed, narrow, containing chlorophyll, and others broader. These latter distinctly exhibit thickening layers, either merely as large pores, which subsequently become actual apertures, or, as in *Sphagnum*, also spiral fibres; they lie either in the same plane with the green cells (*Sphagnum*), or they cover the reticular layer of green cells on both surfaces, in layers varying from one to five. Much contention has been kept up, by Meyen especially, concerning the structure of the *Sphagnum* leaf; but this must be considered to be wholly set at rest by Mohl.†

The stomata on the capsule of Mosses, however simple the subject may be (there being really not the *slightest* difference between these and the openings found in the *Phanerogamia*), have likewise given rise to wonderful discussions; and botanical mystifiers, instead of treating nature simply, as sound sense dictates, have been pleased to express themselves as follows:—"The pores, as peripheric members allied to the spiral vessels, although in their structure they cannot be compared in any respect to the true pores of the epidermis (the reason wherefore neither is nor

* *Leucophaneæ*, according to Hampe.

† Anatom. Untersuchungen über die porösen Zellen von Sphagnum. Tübingen, 1837.

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*a*, Epidermis of the lower surface; *b* and *d*, liber-like cells; *c*, vasculose expanded cells.

141 *Mnium punctatum.* *A*, A section through the margin of the leaf: *a*, leaf-cells; *b*, marginal nerve. *B*, Partition between the leaf-cells in their upper part, very much enlarged. *C*, A few leaf-cells seen from the surface; the fine lines separating the cavity of one cell from the other can easily be explained by a comparison with *B*.

can be explained), yet manifest *a tendency* towards this form." Sad indeed, that men of intellect should seek science amid such a confusion of words! By others, Robert Brown among the rest, stomates have been considered as channels for the evacuation of the spores; this, however, they cannot be, since they never open a communication between the spore-cavity itself and the exterior. The spongy cellular tissue below them always passes gradually into a close cellular tissue, the internal membrane, as it approaches towards the spore-cavity. They do not deviate in the most trifling degree in *Polytrichum alpinum* from the ordinary structure of the stomata, although such would appear to be the case from the incorrect delineation of Treviranus (see as above, fig. 18.). I have myself been unable to examine the pores of the capsule of *Lyellia;* but if the delineation of Treviranus (fig. 17.) be correct, they have nothing to do with the stomata, and are organs of an entirely special kind. I would remark, that, although I am not confident of the fact, I believe I have seen spiral fibres in the cells of the peristome; for instance, in *Hypnum triquetrum.*

## b. *Agamic Plants having Roots.*

## VI. CLUB-MOSSES (Lycopodiaceæ).

§ 104. A perfect history of the development of the *Lycopodiaceæ* remains still a desideratum. Only so much is certain, that in the germination of the larger spores, which will be mentioned, a true root appears. In the perfect plant, the stem, which is almost always recumbent, develops roots on the lower side, along its whole length, and dies off from below upward. The leaves always follow one another closely around the stem, and are sometimes twisted in such a manner as to appear as if they were ranged in one plane on opposite sides of the stem. The branches which are developed from the axillary buds often stand similarly, in such a manner that the ramification is pinnatifid, or the bifurcating branches are erect and arranged in pyramidal forms; in rare cases the stem is flat, and the leaves far asunder, as in *Bernhardia complanata.* The leaves are almost always narrow, lanceolate, similar to the leaves of Mosses, but bearing more resemblance on the recumbent stems (where they evidently stand in two rows) to the leaves of the Liverworts, and are likewise smaller and of different form on the under side of the stem. All are provided with a simple mid-nerve. The greatest deviation is in the stem of the *Isoetes,* which is shortened into a thick disc, and has long, narrow, grass-like leaves, that enclose one another below in a sheath-like manner. In a few of the *Lycopodia,* the axillary buds are developed into a somewhat more fleshy condition in all their parts, and spontaneously (?) separate from the stem to constitute bulbels (*bulbilli*).

It appears to me, that the *Lycopodia* are most nearly allied to Mosses and Liverworts, from the little we as yet actually know of the history of their entire morphological development.* *Isoetes* may constitute a separate family allied to these, or, still better perhaps, be reckoned as belonging to them ; at any rate, a moderately exact comparison will suffice to show that this plant does not belong to the *Rhizocarpeæ*, and that it cannot either constitute a transition stage from any immediately approximate family to the *Rhizocarpeæ*. The *only* resemblance that has led to their being placed together was the circumstance that, in both, the reproductive organs were situated below. (With equal justice *Raja Pastinaca* and the Scorpion might be brought into the same family, since both have a sting in the tail.) But, as the statement was once printed, it availed little that more exact observations showed *Isoetes* to be devoid of any analogous characteristics, or even the most remote resemblance to the *Rhizocarpeæ;* DeCandolle alone appears to have had more correct views on the subject. Link †, a few years ago, again coupled the two together, *invitâ naturâ.*

§ 105. *A.* At the base of the leaves (which are sometimes compressed into a kind of club at the extremity of an extended leafy stem, and assume somewhat different forms), or more rarely in an indentation of the leaves (for instance, *Tmesipteris*), there arises a cellular knob, whose external layers of cells become the wall of the sporocarp, and whose inner cells, as parent cells (*sporangia*), generate four spores each, invested with a peculiar membrane, which seldom exhibits warts or points, after which the sporangia become absorbed. In the *Bernhardiæ* the sporocarps are placed upon the points of the shoots, two or three grown together. The ripe sporocarp is round, kidney or crescent shaped, and tears with a vertical cleft (as in *Lycopodium annotinum*), or a horizontal one (*L. inundatum*), the margins of which are often lobed, (as in *L. canaliculatum*). In *Isoetes* the sporocarps are somewhat immersed in the base of the leaf, and covered by a heart-shaped scale. They contain, among obliquely directed cellular filaments, small cellular sacs, with many small spores exhibiting the ordinary formation, and other sacs which enclose four larger spores, consisting of cells provided with the ordinary integument, and having a thick crust of carbonate of lime (?).

Mohl† has proved, as incontrovertibly as it was possible without

* The interesting experiments on the germination of the larger spores were pursued by Bischoff, and first made known by him; notwithstanding which, he says (Die kryptogamischen Gewächse, p. 97.), "We find no distinctly separated main roots in the *Lycopodia*," because he had only the old developed plant in view. This is certainly a remarkable illustration of the extent to which this routine-like method in science may blind the eyes of people even against their own discoveries.

See Filicum Species in Horto Regio Botanico Berol., Berlin, 1841 ; a work which is twenty years behind the discoveries made in all things relating to general science.

† Mohl, Ueber die morphologische Bedeutung der Sporangien der mit Gefässen versehenen Kryptogamen, Tübingen, 1837, p. 28.

knowing the history of their development, that the sporocarps are definite modifications of the parenchyma of the leaf. An acquaintance with the mode of their development leads, however, to the same results. In *Isoetes* we are still deficient in more exact investigations. It seems to me, however, that, considering the exactly similar structure of the large and small spores, the difference of size, and the investment of (probably) carbonate of lime, together with the somewhat greater complexity of the fruit owing to the persistence of the cellular tissue, are matters of very subordinate importance. Here, too, we must seek for elucidation solely from the history of development.

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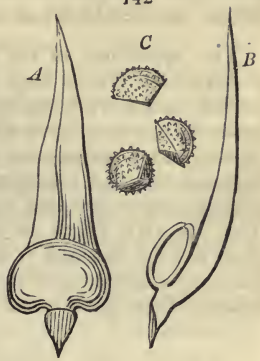


*B.* In some of the *Lycopodia* we meet with another form of the fruit, which is rounded, tetraedric, opens by a longitudinal cleft into two trilobed valves, and encloses four large spores, which consist of one spore-cell and a very tough investment covered with warts or reticulate striæ. The contents, according to Bischoff *, are a delicate cellular tissue.

The large spores are certainly identical with the large spores in *Isoetes;* and if even their contents be cellular, this must be merely owing to a further stage of development. †

§ 106. The stem of the *Lycopodiaceæ* consists of a mass of rather loose parenchyma, intersected by a central simultaneous (§ 26.) vascular bundle. This vascular bundle generally has the vessels scattered through it in irregular lines and bands, and mostly surrounded by a deposit of brownish thick-walled parenchyma. The vascular bundles, passing into the leaves and lateral stalks, often run in an oblique direction through the parenchyma, separating from the principal bundle a long way below where they pass off into the leaf. The leaves consist of several layers of roundish parenchyma, intersected by a vascular bundle, and invested by an epidermis exhibiting stomata on both surfaces. The wall of the sporocarp has mostly two layers, the external one displaying flat cells with tough curving lateral walls, and the inner thin-walled

* Bischoff, Die kryptogamischen Gewächse, p. 110.

† The *Lycopodiaceæ* were the only cryptogamic plants against which the anther-mania had not been directed; when (Jan. 18. 1842) Link, not content with his discovery of antheridia in Lichens, likewise provided the *Lycopodiaceæ* with antheridia, which he maintained were the larger spores. (Froriep's Notices, vol. xvi. p. 74.) Men are always nearest to a new stage of advancement when they have carried out a definite folly in all its systematic completeness. Now, therefore, when there remain no further antheridia to be discovered, it is to be hoped that this worn-out plaything will be cast aside.

142 *Lycopodium annotinum.* *A*, The spore-leaf, with the capsule; *B*, the same in a longitudinal section; *C*, spores (*semen Lycopodii*).

cells. In *Lycopodium inundatum* the inner cells exhibit thick annular fibres, similar to what we find in the fruit of the Liverworts.

The epidermis of the upper and lower surface of the leaves in *L. stoloniferum* differs very much. The cells of the upper one are thicker walled, and have lying upon them, here and there, long cells, which are beset on the outer side with from two to three rows of warts. The cells of the under surface are thinner walled, and contain chlorophyll; while between the two a somewhat spongy cellular tissue is interposed. The stomata are *only* found upon, and close to, the leaf-rib of the *Lycopodia.* The annular fibres in the capsule-wall of *L. inundatum* were first observed by Bischoff*, who, however, gives an incorrect and very far-fetched explanation of them, that might be at once refuted by a consideration of their early condition.

## VII. FERNS (Filices).

§ 107. In the germination of the Ferns the spore-cell breaks through the external membrane and expands, in some even at an absolutely definite, previously indicated point, into a longer or shorter tube, whose extremity forms new cells, which gradually arrange themselves into a flat, generally bilobed, proembryo; a few of these cells expand downward into adhering fibres. At a definite part of this proembryo there is formed a group composed of thicker cellular tissue, and, by degrees, a small ovate corpuscle, one extremity of which is prolonged into a root, and the other into a bud, forming the stem and leaf.

The stem then assumes two essentially different modifications, in one of which it does not expand, and in the other of which it does so to a great length between every two succeeding leaves (which are always closer together at their first origin than they appear subsequently). In the first case the stem mostly creeps subterraneously, so that the leaves alone appear above the ground, as in *Pteris aquilina,* or it creeps upon the ground or up trees and rocks (as in *Lomaria scandens*); in the second modification it again exhibits two further differences, according as the root, and subsequently the stem, constantly does or does not die off from below. In the former case it rises but inconsiderably above the earth, occasionally lying obliquely in it (as in *Aspidium Filix mas*); in the latter case it grows (but only under the tropics) into a considerable sized trunk, some twenty or thirty feet in height (tree-fern, as, for instance, *Cyathea, Dicksonia, Alsophila,* &c.). Almost all stems exhibit adventitious roots (*radix adventitia*), arising in a peculiar manner from the stem, and occasionally investing the trunk with a thick network (as *Cyathea Schansin*).

The leaves of Ferns are mostly stalked, seldom sessile, generally divided into lobes at the margin (occasionally in the most various

* Die kryptogamischen Gewächse, p. 109.

and beautiful manner), seldom simply undivided, always flat, and having vascular bundles (nerves, *nervi*), the ramifications of which are varied and elegant. The leaf is generally connected by a continuous cellular tissue with the stem, on which account the older leaves only wither, to the lower hard part of the leaf-stalk, without falling off. Occasionally, but rarely, a layer of early-withering cellular tissue forms a true articulation (*articulatio*), so that the leaves become detached from a defined surface (as in *Cyathea arborea*). Such an articulation (?) never occurs in the continuity of the same leaf, and on this account there are no true *folia composita* in Ferns.

Buds are, on the whole, but seldom found in the leaf-axils; yet they do occur, as, for instance, in the case of *Aspidium Filix mas.* On this account the stem of Ferns is mostly simple, and always so in the tree kinds. Here, too, a furcate division of the stem at it apex appears to take place without any axillary buds, as in *Polypodium ramosum.* In the axillary buds, as well as in the terminal bud of the stem, the leaves are rolled together in a spiral manner (circinate æstivation, *æstivatio circinata*).

In a few tropical Ferns small hollows occur in the axils of the leaves, at first covered by the epidermis, and filled with a peculiar spongy cellular tissue. Hairs and glands are more rarely met with in Ferns, while, on the contrary, all are more or less covered with small, quickly-withering scales (*paleæ*).

The other extremity of the young plant developes itself downwards into the earth as a multifariously ramified root, which, as already remarked, soon dies off again in many of the Ferns.

It frequently happens that individual cells, or groups of cells of a leaf, separate from the individuality of the whole plant, form tubers, and subsequently grow independently into a new plant. These young plants are formed from the leaf-surface, and especially in the angles of the division of the leaf.

We have some beautiful investigations, as, for instance, those by Kaulfuss*, on the first development of the plant from the spore (fig. 143.);

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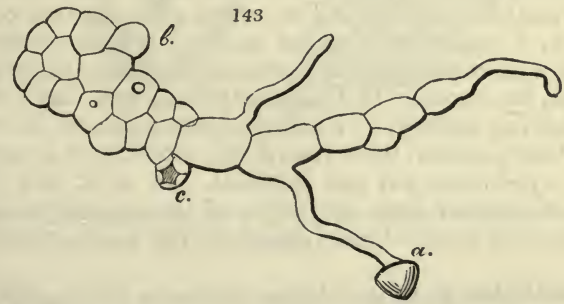


* Das Wesen der Farnkräuter, &c., Leipzig, 1827.

143 *Pteris speciosa.* *a*, Germinating spore; *b*, early condition of the proembryo; *c*, antheridia.

but even these are very far from being complete: there is no reference whatever made here to the first origin of the new cells. There is, however, some importance to be attached to the observation, that there appears in the proembryo an ovate corpuscle free at both ends, which naturally, therefore, remain capable of propagation in opposite directions, by which the morphological distinction of stem and root (fig. 144.) first appears in the series of vegetable forms. Our knowledge regarding the extensive history of development is, however, very deficient, and we need far more exact and fundamental investigations on the relation of stem and leaf, as well as on the formation of the furcated divisions of the stem and the germination, since without such observations little that is of importance can be said upon the subject.

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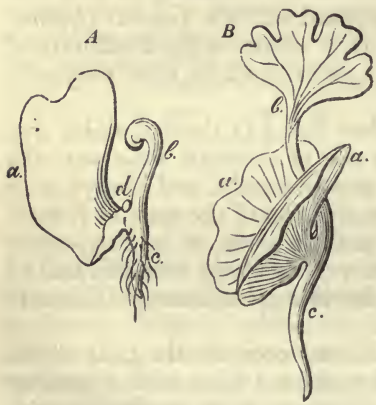


The morphology of leaf and stem, as far as it is applicable to Ferns, must be derived from the *Phanerogamia*; the term frond (*frondes*), as applied to the leaves, is here quite superfluous.

We know, as yet, nothing of the signification of the accumulation of pulverulent cells * in the axilla of tropical Ferns, which Von Martius once asserted, without any reason, to be antheridia; they may perhaps be wholly analogous to the lenticels of *Phanerogamia* (see below).

§ 108. *A.* In all cases spores are formed in the tissue of a true leaf, which either appears wholly unchanged or is attenuated by the non-development of all or of the most superfluous part of the parenchyma around the principal nerves: I call it the spore-leaf (*sporophyllum*). Where it differs but little, or not at all, from the ordinary leaves, it shows upon the back, or on the margin, differently formed, scattered accumulations (*sori*) of sporocarps, which are generally entirely or partially covered by a definitely formed fold of the epidermis (the *indusium*). The several sporocarps are commonly fastened to a somewhat elevated mass of cellular tissue, which appears as a short pedicle or as a seam, more seldom as an elongated pedicle (as, for instance, in *Hymenophyllum*), and they are formed in the following manner: — From the parenchyma of the leaf (that is, from those pedicles) there rises a cell, which soon separates into two, one cylindrical and one spherical. In both, new cells are formed; in one they form the pedicle of the sporocarps, the others fill the spherical terminal cell (*capsula*); the most external consti-

* Compare H. Mohl, De Structura Filicum Arborearum, Monach. 1833, p. 7. § 12.

144 *Pteris spec.* *B*, Germinating plant: *a a*, the two lobes of the proembryo; *b*, the first leaf of the young plant; *c*, the root. *A*, A longitudinal section of a somewhat earlier germinating plant: *a*, lobes of the embryo; *b*, first leaf of the plant; *c*, root; *d*, terminal bud.

tute a cellular wall, and the internal ones parent cells (*sporangia*) for the spores, being absorbed soon after the latter are perfectly developed and have been invested with a special membrane covered with warts or folds. From the parietal cells a series of cells is formed, running either vertically or obliquely from the pedicle almost entirely round the capsule, or forming a horizontal zone at a greater or lesser distance from the top of the capsule, and in such a manner that its inner, and upper and lower contiguous walls become very much thickened, while the other walls remain thin. These cells constitute what is termed the ring (*annulus*); by its unequal contraction in drying, the capsule is opened for the escape of the spores. In other Ferns the small quantity of parenchyma developed around the nerves forms in its interior groups of parent cells and spores, so that the lobules of the leaf swell spherically into capsules, and, occasionally bursting open by means of an imperfectly completed ring, shake out the spores (as, for instance, in *Ophioglosseæ*, *Osmundaceæ*).

*B*. It is only in the proembryo of Ferns that we find organs similar to the antheridia of Mosses and Liverworts; here they occur either upon the margin or upon its upper surface, and are most spherical and unpedicled.

By way of illustration of the above, I will give circumstantially the delineation of a part of the spore-leaf of *Pteris chinensis* (fig. 145. *A*, *B*),

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and of *Adiantum pubescens* (fig. 145. *C*), as well as an analysis of the capsule of *Scolopendrium officinarum* (fig. 146.).

[145] *Pteris chinensis*. *A*, Part of the spore-leaf: *a*, *b* designates the direction of the section. *B*: *a*, *b* is the leaf; *c c* its thickened margins; *d d*, folds of the margins (indusia); *e e*, capsules. *C*, Part of the spore-leaf of *Adiantum pubescens*, with some sori, or heaps of sporocarps, covered with reniform indusia.

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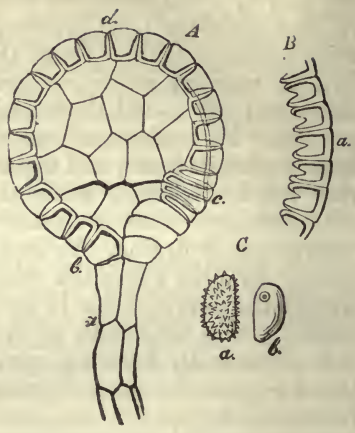



The easily-traced history of development of the capsule (as I have given it according to my observations on *Blechnum gracile*) relieves me from the necessity of wasting one word in refuting the imaginary origin of the capsule from a leaf rolled inward, and which, of course, has been duly derived from a fantastic imagination.

Mohl* has refuted this and the other view, that the sporophyll is formed by the blending of a leaf and a twig; entering into the subject with more profoundness of argument than such unscientific sports of fancy, in my opinion, merit, and, with his ever-manifest acuteness of comprehension, has applied the results of his own excellent investigations to develop the simplest and most natural, and consequently also the only true, view of Fern fruits. The *formal* mania for discovering antheridia in the *Cryptogamia* for a long time failed to find support in the class of the Ferns; for stomates and the groups of spiral cells in which the spiral vessels of the leaf-nerves terminate, the indusium, and other parts, although termed anthers, could not for any length of time be maintained to be such. Fortunately for those who delight in sporting with words without affixing any definite ideas to them, a few glandular hairs (cells, of which the last, which was spherical or ovate, contained some gum and mucus) were found near the capsules in some specimens of Ferns; they were pronounced to be anthers, and the discoverers rejoiced in the self-satisfaction of having followed the course of science. *Habeant sibi!* I can corroborate the fact of there being glandular hairs in many Ferns, and, indeed, on the very peduncle of the sporocarps, but they are decidedly wanting in the case of a great many others. For my part, I am surprised that no one has as yet insisted upon the presence of the organs of sense, as eyes and ears, in plants, since they are possessed by animals; such an assumption would not be a bit more absurd than the mania of insisting upon having anthers in the *Cryptogamia*, simply because they are found in the *Phanerogamia*.

We are indebted to Nägeli† for the discovery of the antheridia. It is very easy to confirm his assertion by direct observation (fig. 143.). They do not differ essentially from those of Mosses and Liverworts.

§ 109. The stem of Ferns consists of a mass of parenchyma, traversed by simultaneous vascular bundles (§ 26.), and may, when

* Mohl, Morphologische Betrachtungen über das Sporangium der mit Gefässen versehenen Kryptogamen, Tübingen, 1837, p. 11.

† See Zeitschrift für wiss. Bot. von Schleiden und Nägeli, vol. i. part i. p. 168. (1844).

146 *Scolopendrium officinarum.* *A*, The ripe capsule: *a*, the pedicle; *b*, *d*, *c*, the ring; *c*, the place where the capsule is torn open. *B*, Part of the ring of a capsule that is burst open: *a*, the side turned from the capsule. *C*: *a*, the spore; *b*, the same (after the removal of the external membrane) with a cytoblast.

the latter are in a more or less closed circle, be distinguished into *medulla* in the interior and *cortex* in the exterior. The vascular bundles lie in their vertical course alternately side by side, so as to form a net, the meshes of which furnish, at their upper part, branches of the bundles to the leaves and branches, where the latter are present; we find a few isolated vascular bundles in the medulla of the arborescent Ferns, which pass out through those meshes into the leaves. The vascular bundles have often a band-like, or channel-shaped form, compressed from within outwards; and are generally surrounded by a sheath of thick-walled elongated cells coloured brown (by tannin and humic acid?); and bundles of such cells alone also traverse the stem. The parenchymatous cellular walls, on dying, speedily acquire a more or less dark brown colour. It is well known that many Ferns contain a large quantity of tannin. The parenchyma, especially the base of the leaf-stalk, often contains much starch (as, for instance, in the *Marattia cicutæfolia*), which serves in some of the South Sea Islands as an article of food. The vascular bundles are composed of porous vessels, having the pores small, or most frequently with slits; sometimes, however, as in the leaf-stalks, we find spiral vessels which admit of being unrolled. The leaves but rarely consist of one single cellular layer (such being only the case in the *Hymenophylleæ*), but generally of several, forming two laminæ: an upper one, composed of short cylindrical cells, vertical to the surface of the leaf, and an under one, formed of loose spherical, or sponge-like, parenchyma. Moreover, the two sides are invested with a true epidermis, which always exhibits perfect stomata on its lower surface. The upper epidermis not unfrequently consists of several layers of cells. Isolated bundles of liber cells are often met with above and below the vascular bundles of the leaves. The leaves contain a large quantity of potash salts.

The attempt to represent the stem of the Fern as merely composed of leaf-stalks grown together is so entirely at variance with the law of its development, and, consequently, so totally devoid of foundation, that we do not deem it worth while to contest the point. Germination shows that there is a rudiment of the stem prior to the formation of the leaves and leaf-stalks. We may refer for the anatomy of the stem to Mohl's work, which we have already mentioned, and which certainly still leaves much to be done, although he can scarcely be blamed for the deficiency. We now feel the want of the history of the living development, and a much greater service would be rendered to science if one of the many travellers in Brazil would furnish us with the result of an accurate investigation of this development in the stem of an arborescent Fern, instead of adding a couple of thousand dried new species to the 80,000 which we already possess, and which are scarcely worthy of notice while we continue, as at present, hardly to have a certain knowledge of any one single specimen. The annulus of the sporocarp exhibits a structure similar to the teeth of the fruit of the Mosses. I think I have detected very delicate spiral fibres in the cells of the walls of the fruit in *Ophioglossum* and *Osmunda*.

## VIII. THE HORSETAILS (EQUISETACEÆ).

§ 110. The spore-cell of the *Equisetaceæ* expands into an utricle, at one extremity of which new cells are formed, that gradually acquire the form of a many-lobed flat expansion, a simple cellular layer, several cells of which become elongated into filiform adhering fibres (the *proembryo*). At one point of this proembryo there appears a cellular node, which develops itself upwards into the bud, stem, and leaf, and downward to a root. The main stem appears, however, to die off very speedily in the case of most, while in its place are developed from the axillary buds of the first leaves lateral branches, which run horizontally below the surface, never assume a green colour, and whose lateral branches partly rise in a vertical direction, and appear above the ground. All the stems of the *Equisetaceæ* are round, mostly furrowed and regularly elongated between the successively ranged leaves (*internodium*, internode). At the roots of the leaves the stems are somewhat contracted, and easily break off (*nodi*, nodes). The leaves are small, scaly, ranged in a whorl, and grown together by the lower part of their margin into a sheath closely surrounding the stem. The axillary buds of the stem above ground burst in a remarkable manner *through the base of the leaves*, and form whorls; these have also, less frequently, lateral branches. The individual lateral branches are not invariably elongated, but enlarge spherically between every two circles of leaves, become fleshy, and then readily separate from the stem into their individual joints.

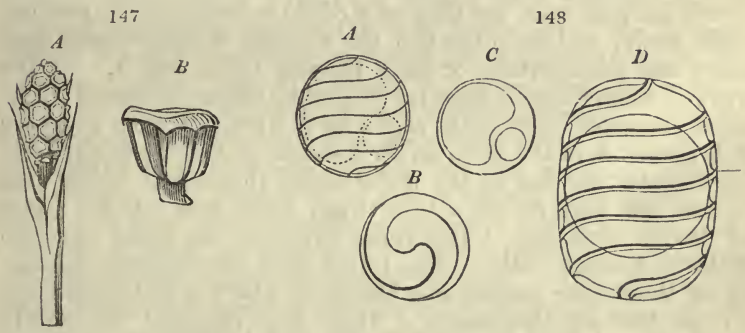
I have not myself enjoyed any opportunity of observing the germination of the *Equisetaceæ;* and the description given is taken from Vaucher* and Bischoff.† But both leave very much to be desired. It is inconceivable to me how any one can say "new cells appear, new cells seem to occur between," without even touching upon the obvious inquiry "whence come these cells?" It is an evidence of the difficulty that there is in giving a correct account of what we have observed; and assertions of this nature are all but untrue, since it merely amounts to this, that in one case he saw a few, and in others many cells, the position and interposition of the cells originating in fancy and not from observation. We must remark, that in the primary stem the first leaf-circles are scarcely removed from each other, and that the expansion of the internodes of the stem begins higher up.

§ 111. At the points of the stems above ground, or of their branches (often in peculiar branchless stems), several closely contiguous leaf-whorls become developed into an ovate fructification. The individual leaves (*sporophylla*) change in a peculiar manner, assuming the form of a hexagonal disc, attached by a pedicle at its

* Mém. de Mus. d'Hist. Nat. vol. x. p 429.
† Die kryptogamischen Gewächse, p. 40, et seq.

centre. From five to seven hemispherical sporocarps are developed from and upon the lower and inner surface of the disc. Two layers of the cellular tissue of these form the wall of the fruit. The inner cells become parent cells (*sporangia*), and from each of these one spore is produced from a distinct cytoblast. Two spiral fibres are simultaneously formed in the parent cell, which at first completely cover the inner wall, are rounded off at both extremities, and somewhat flattened out, and are firmly closed together. The spiral coils are subsequently somewhat separated by the expansion of the parent cell. When the spores are quite mature, the hygroscopical spiral bands tear the delicate wall of the parent cell, and wholly separate from each other, although they remain adhering by the centre to the spore. The sporocarps then split longitudinally, and emit the spores.

The whole fructification of the *Equisetaceæ* (fig. 147. *A*, *B*) is not to be distinguished — setting aside the actual development of the parent cells of spores (fig. 148. *A*—*D*) from the antheriferous inflorescence of




*Taxus** — by any morphological or anatomical characteristic, on which even a merely specific distinction can be established. This peculiarity was, however, for a long time put under contribution by the fancy of botanists, and, as may naturally be supposed, the antheridia mania did not suffer the *Equisetaceæ* to escape. As nothing else appeared, the unfortunate spiral fibres were chosen, as occasionally a few mucus granules might be seen adhering to them. As early as 1833† Mohl gave a correct explanation of these, and I myself had often followed the history of their development, which it is extremely easy to do, always arriving

* Compare also Mohl's Sporang der Kryptog. p. 7.

† Mohl, Flora of 1833, on the Spores of Cryptogamic Plants, p. 15.; and the work before quoted.

147 *Equisetum limosum.* *A*, Fruit-bearing extremity of the stem. *B*, Separate spore-leaf, seen from the side; magnified strongly.

148 *Equisetum arvense.* *A*, Young mother-cell, with a spiral layer of thickening: the dotted lines show the spore shining through, with its large cytoblast. *B*, The same mother-cell, seen from above. *C*, The spore from it. *D*, Completely developed mother-cell, with the spore in it; *a*, interval between the turns of the spiral fibres.

at the same results, although at the time I was unacquainted with Mohl's observations. That Link*, in the year 1841, should speak of antheridia in a work where one might expect to find not only a complete use made of the materials at the author's command, but likewise a thorough investigation of the subject treated of, makes one almost envy the man who knows how to make work a matter of so little moment. Meyen says nothing of this subject, the *Lycopodiaceæ* and *Equisetaceæ* not being treated of in his *system* of Physiology.

§ 112. The stem of the *Equiseta* consists of a somewhat lax parenchyma, separated by a circle of from six to ten successive closed (?) vascular bundles (§ 26.) into medulla and cortex. In the underground stem the external cortical cells become by degrees more tough in the walls, and porous. Air-cavities occur alternately with every two vascular bundles, formed in the cortex by the laceration and resorption of the cellular tissue. A similar opening occurs in the axis of the medulla. The vascular bundles are developed from within outward, contain, most internally annular vessels, then spiral vessels, and finally porous vessels. The first portion formed soon dies off, the cells tear, and thus an air-hole is formed in the vascular bundle itself; and we often find the annular or spiral vessels projecting into this aperture, or their remains fallen into it. In the furrowed stems there lie upon the projecting ridges bundles of thick-walled, elongated (liber) cells; such a layer often appearing under the whole epidermis of the stem, as, for instance, in *Equisetum fluviatile.* The vascular bundles at the nodes range themselves closely into a circle, and give off from here twigs, which pass into the leaves and lateral branches. The parenchyma at the nodes has also smaller and closer cells. The leaves have one vascular bundle, and on their outer surface one bundle of liber; and between the two we find an air-passage. Their free unjoined extremities are mostly, with the exception of the middle part, composed of two thin cellular layers, dry and membranous. They are furnished in the middle, like the stem itself, with an exceedingly firm epidermis, which distinctly exhibits stomata, arranged mostly in rows, and whose cells are for the most part thickened towards the exterior in a wart-like manner. In the cellular walls, especially in these wart-like projections, we find deposited a large quantity of silica, in the form of small lamellæ, which may be isolated by means of concentrated sulphuric acid, which only destroys the vegetable substance; they unite, however, on being heated from the action of the potash salts present, and then retain in the ashes the perfect forms of the living plants.† The inner layer of the wall of the sporocarp is formed of the most beautiful spiral fibrous cells. The spherically enlarged stems below the surface contain, in a close cellular tissue, starch (?) and oil, and have only very small, imperfectly developed vascular bundles.

* Link, Filicum Species, &c., p. 9.

† Struve, De Silicia in Plantis nonnulla. Berlin, 1835.

One peculiarity I often met with in the subterraneous stems. The somewhat elongated cells which bound the air-passages, at a late stage begin to develop cells in their interior. These penetrate particular places in the wall of the mother cell, and project as utricles into the air-cavities, then expand into a perfectly globular form, become cut off by constriction, and thus fill the air-space up a second time with lax globular cellular tissue. I cannot yet decide whether this is a diseased or a regular structure.

## B. Sexual Plants (*Pl. gamicæ*).

§ 113. The sexual plants are at once characterised, as a large and connected division of the vegetable kingdom, by the peculiar manner in which a new individual is formed, and by the double and essentially distinct organs which are required for this purpose. Firstly, they develope four cells, clothed by a peculiar membrane, within a mother-cell (*sporangium* of the *Agamæ*), which becomes absorbed subsequently, so that the former, when perfectly mature, lie free in a little sac composed of cells (*sporocarp* of the *Agamæ*). This sac is called the anther (*anthera*), the spores are called pollen or pollen-granules (*granula pollinis*), and the special membrane by which they are clothed is the external pollen-membrane. Secondly, they produce a cellular body free in any case at the apex, of oval or elongated form, in which one cell becomes so much enlarged that it causes the absorption of a part of the surrounding substance, and thus a considerable cavity is produced in the body. This body is called the seed-bud (or ovule) (*gemmula*); the great cell is the embryo-sac (*sacculus embryoniferus*). The sac contains cytoblastema, from which (excepting in the *Rhizocarpeæ*) new cells are formed, gradually filling the embryo-sac, until, as sometimes happens, the growing embryo again displaces them. The development of the new plant proceeds by the expansion of the cells of the pollen-granules into a tube, which under favourable circumstances penetrates to the embryo-sac. The other end of the pollen-tube dies away while the extremity in the sac developes new cells, which become arranged into the form of the rudimentary plant, the embryo.

I have here only drawn attention to those points admitted with respect to the Phanerogamic plants by all the best observers of recent times. (With regard to the *Rhizocarpeæ*, see the special explanations.) I have here displayed the essential facts, namely, the analogy of the course of formation and the nature of the pollen with those of the spores of the *Agamæ*, and the wholly similar conversion of the pollen into a tube, of which one end (though it must be freely admitted that we do not know precisely how) forms new cells, which gradually arrange themselves and form the new plant, while the other end dies away; comparing this with the germination of Mosses, Ferns, &c.: and, while I have distinctly marked this comparison, it will at once have become evident what new phenomenon is met with in the sexual plants, namely,

the appearance of the seed-bud (ovule), within which alone the development of the appointed end of the pollen-tube into a new plant can take place. Directing our attention to the universally occurring, and consequently essential, characteristics presented by the seed-bud, namely, the disproportionately great developement of one single cell (the embryo-sac) within a cellular body free at one end and containing cytoblastema, out of which, at least in all the *Phanerogamia*, cellular tissue is formed, there is clearly displayed an analogy, which can scarcely be mistaken, with the antheridia of the Mosses and Liverworts; and we have in this structure an interesting example in the vegetable world, of a fact often presenting itself in the animal kingdom, namely, a determinate product of the formative force (a morphological organ) present in one group, without possessing the same physiological importance which it has in another group, and without the morphological organ becoming a physiological organ. On the other hand, when we have conceived the comparison in these two large groups, we may make the reasoning, evidently deducible from the resemblance, of service as a safe point of departure from which to arrive at further analogical conclusions. If we have identified the pollen-grain and the spore, and if we have found their development into new plants to be similar in the main points, we may venture to expect similarity in the less important particulars. It is now certain that in the *Agamæ* one end of the tube of the spore (as in the Ferns and *Equisetaceæ*) can, without the aid of any other organ, develope new cells as the foundation of a new plant. Hence, I seek in the *Phanerogamia* also the essential cause of the formation of new cells, and consequently of an embryo, in the power of development of one end of the pollen-tube, which is perhaps called forth and modified by the action of the embryo-sac, but which appertains simply and exclusively neither to this nor its contents. We do not by this means acquire any results as to the nature of the sexual plants, yet we do gain a valuable leading principle to guide us in further researches, and in the critical examination of the results obtained. Thus, the opinion which I delivered on the formation of the embryo of the *Phanerogamia* would have been justified, even if decided observation did not support me, and if Meyen * had been right in asserting that the new cells are formed externally on the apex of the pollen-tube (and not in the inside of it, as I have *seen*). This mode of formation might occur in the *Agamæ*, as, for instance, Mirbel actually asserted in his work, already referred to, on *Marchantia*, which researches I indeed must consider very imperfect. On the other hand, the opinion that the first cells of the embryo are not formed inside the embryo-sac, while the pollen-tube remains outside it, is supported by the analogies to be drawn from the investigation of the *Rhizocarpeæ*, where the embryo is undoubtedly formed by the end of the pollen-tube, outside and scarcely in immediate contact with the embryo-sac; leaving out of consideration the improbability that, in this process, three forms so essentially different should be exhibited, without even being respectively confined to definite groups, as Meyen † must allow from his own researches.

§ 114. All sexual plants possess stem and leaves, the latter at

* Physiologie, vol. iii. p. 307, et seq.

† Physiologie, vol. iii. p. 307, 308., compared with 310, 311., and, still more decidedly, 313.

all events, in the parts of the flower. In the *Phanerogamia* the anther is unquestionably only a modified leaf, the seed-bud (ovule) probably only the modified extremity of a stem; in the *Rhizocarpeæ* no explanation of the kind can be given, from the imperfect knowledge of the course of development.

### a. *Plantæ athalamicæ.*

§ 115. The character of this group, and the distinction from the *Phanerogamia*, is the fact that the seed-bud (ovule) and pollen separate as independent bodies from the plant, and the tubular expansion of the pollen-cell penetrates the seed-bud subsequently, and then becomes developed into a perfect plant in *one* act of vegetation.

## IX. RHIZOCARPEÆ.

§ 116. In the *Rhizocarpeæ* two very distinct parts become detached from the old, in order to the production of a new individual, namely, pollen-grains and seed-buds (ovules). The former have the usual structure, consisting of a single cell (pollen-cell), with an external pollen-membrane. The others present the following structure:—a very large cell, with firm walls, containing large grains of starch, mucilage, and oil (the *embryo-sac*), is surrounded by a white, coriaceous membrane, which is formed of very minute, scarcely distinguishable cells; this membrane forms, at one extremity, a papilla (*nucleus*), which is covered sometimes by three lobes of the same membrane (in *Salvinia*), or by these three united into an envelope open at the point (in *Marsilea*), which is called the simple coat of the bud (*integumentum simplex*). The whole is enclosed in a cellular sac, the sac of the seed (*sacculus*) (as in *Salvinia*), or in a layer of cells so gelatinous as to be almost confluent (as in *Pilularia* and *Marsilea*). The cell of the pollen-granule extends itself into a tube of variable length (long in *Salvinia*, shorter in *Pilularia*). During the same time the cells of the nucleus are developed near the apex of the embryo-sac, become clearly distinguishable and laxer, filled with chlorophyll, and at length break through the nucleus, so that they project free, forming the nuclear papilla (*mammilla nuclei*). If a pollen-tube now comes in contact with these cells, it penetrates deeply between them until it reaches a layer of small green cells which covers the embryo sac (*Pilularia* and *Salvinia*), and then it expands in a vesicular form, displacing the surrounding cellular tissue, which, however, continues to be developed, and projects from the seed-bud as a green body of variable size. In *Salvinia* it forms two depending lateral processes, while in *Pilularia* a portion of the superficial cells become elongated into capillary filaments. In the vesicular extremity of the pollen-tube cellular tissue is

developed, which, taking the form of the embryo, one end finally breaks through nuclear papilla of the seed-bud, which up to that time appeared as a thin-walled sac, and now assumes the form of a round sheath (*Pilularia*), or a flattened, bilabiate body (*Salvinia*). In *Salvinia* the embryo, when it emerges, produces a pedicle which expands above into a flat discoid body, swimming on the water (first leaf, *cotyledon*), from the point of attachment of which, below a vertical slit in the same, a bud previously existing in a rudimentary condition develops into a little stem clothed with leaves on both sides, and sending out adventitious roots below. In *Pilularia* the projecting end of the embryo develops into an upright filament of a green colour (first leaf, *cotyledon*), at the base of which a pre-existing bud develops into a stem with long filamentous leaves. The part of the embryo opposite to the protruding end becomes the root, and breaks through, at a later period, the green papilla of the seed-bud, which also then appears like a sheath. Full-grown plants of *Pilularia* and *Marsilea* grow in boggy ground. Their slender stem runs horizontally forward with elongated internodes, producing at the side, and always somewhat to the under side of the clavate expanded apex, leaves which in *Pilularia* are filiform, in *Marsilea* consist of a long stalk (*petiolus*) and a four-lobed blade (*lamina*); on the under side the stem constantly shoots forth adventitious roots, branches by the development of axillary buds, and apparently also by a bifurcating division of the apex of the stem. *Salvinia,* on the other hand, floats freely on the surface of the water; its equally slender stem, with short internodes, bears on both sides shortly-stalked, flat, ovate leaves, sends down adventitious roots in the water from the fruit-stalks, and ramifies little by development of axillary buds. *Azolla,* a tropical genus, resembles a delicate floating Liverwort. Its course of development is as yet wholly unknown.

When in the year 1837*, in my survey of the history of development, I observed that I believed that, with respect to the *Rhizocarpeæ* in particular, much yet remained to be investigated, I had three points in view; first, the peculiar formation of the reproductive organs, described indeed by many, but by no one properly understood; secondly, the inconceivable imperfection of all preceding accounts of germination; and, thirdly, an isolated observation on *Salvinia.* In reference to the first point, the essential resemblance of the so-called large spore to the seed-bud, and of the smaller to the pollen-grain of the *Phanerogamia,* appeared especially remarkable. Touching the second point, it struck me that the germination indicated either the simple development of a plant already perfectly organised in a rudimentary condition (in the *Phanerogamia*), or the development of a single cell into a new plant (in the *Cryptogamia*); but that in the treatises upon the germination of the *Rhizocarpeæ* there had been no idea either of demonstrating the existence of an embryo capable of development, or of tracing a single spore-like cell in its

* Wiegmann's Archiv, Jahrg. 1837, vol. i. p. 316. Schleiden's Botanischen Beiträg. vol. i.

gradual evolution into a plant. Finally, in the third place, I had seen, in a transverse section of a seed-bud of *Salvinia*, which had lain some time to germinate in water, a filiform cell which ran obliquely through the green cellular tissue from a somewhat lateral point of the embryo-sac, and hung out considerably beyond the seed-bud, but appeared to be torn away here. As soon as I had an opportunity, I made a minute investigation, and soon had the satisfaction of discovering the whole process of germination, such as I have described it in the paragraph, first in *Salvinia*, and afterwards, with less trouble, of confirming it, in *Pilularia*. In *Salvinia*, with the exertion of all my patience, I have only succeeded three times in making the section so fortunately as to lay open the entire course of the pollen-tube. Since it runs obliquely, and the minute seed-buds present externally no points by which they can be held, the section becomes naturally a matter of chance. In the somewhat later stage of development of the seed-bud the form of the nuclear papilla becomes a sufficient guide for an accurate section. In *Pilularia* (fig. 149.), on the

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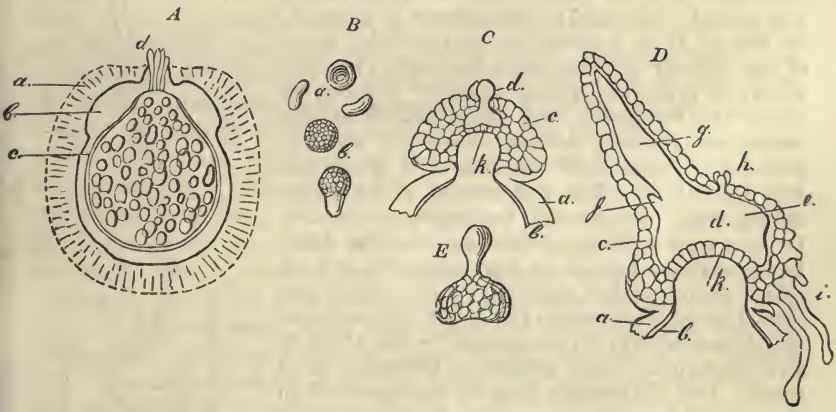


contrary, I have often succeeded in extracting, in a free condition, the pollen-grains (fig. 149. *B*) with the vesicular expanded extremity of their tube (*E*) in the seed-bud (*C*) perfect and uninjured. Here it is not very difficult to trace the whole course of development. Three or four pollen-tubes usually penetrate into one seed-bud here, but only one passes deeply down and becomes the embryo (fig. 149. *B*, *b*, *C*, *d*, *E*):

[149] *Pilularia globulifera*. *A*, Transverse section through a seed-bud at the commencement of development: *a*, gelatinous coat; *b*, coriaceous coat; *c*, embryo-sac, filled with starch and oil-globules; *d*, nuclear papilla. *B*, Pollen grains: *a*, fresh from the pollen-sac; *b*, swollen in water, and beginning to produce tubes. *C*, Upper part of the seed-bud, after the penetration of the pollen-tube (*d*): *a*, coriaceous coat; *b*, embryo-sac; *c*, nucleus and nuclear papilla; *k*, layer of cells which separates the pollen-tube from the embryo-sac. *E*, Pollen-tube prepared free, from *C*: at the upper part it exhibits the now uncovered portion which was enclosed in the outer pollen-membrane; in the middle, the slender, proper tube; and below, the broadly expanded portion, now filled with cellular tissue, which developes into the embryo. *D*, Upper end of the seed-bud, in a still more advanced condition: *a*, coriaceous coat; *b*, embryo-sac; *c*, nucleus and nuclear papilla expanded into a sac, through the development of the embryo; *d*, stem-end of the embryo (*e*); *g*, first leaf (cotyledon); *h*, pollen-tube; *f*, first axillary bud; filiform elongated external cell of the nucleus; *k*, layer of cells, which separates the embryo from the embryo-sac.

from the shortness of the pollen-tube the granules themselves are situated quite near, upon the seed-bud; by degrees they lose their external membrane, and then appear, like three or four pyriform utricles, issuing from the seed-bud (fig. 149. *D*, *h*), which Müller* actually imagined them to be. The course of development of *Marsilea* I have not yet had the opportunity of making out; what Esprit Fabre† has published on the subject I unfortunately only know from Meyen's Year Report‡, where the account, whether from the fault of the author or the reporter I know not, is very superficial and imperfect. The great agreement of the structure with *Pilularia* leads to the expectation that no essential deviation will be found to exist. There are two more points connected with the course of development to which I must call attention. The pollen-tube, as has been stated, does not come into immediate contact with the embryo-sac, since the apex of the latter is closely invested by a simple layer of green cells (fig. 149, *C*, *k*, *D*, *k*). Before the nuclear papilla is fully formed, the membrane of the embryo-sac is very tough, and almost coriaceous; subsequently it expands, so far as it is covered by that cellular layer of the nuclear papilla, hemispherically (in *Salvinia*), or even into a long cylinder rounded off above (in *Pilularia*), and thus exhibits at this region an extremely delicate membrane, which is continuous below with the unaltered tough one (fig. 149. *D*, *b*). The pollen-tube, which penetrated and has become vesicularly expanded, forms a very delicate investment over the developing embryo for a long time after (fig. 149. *e*), which even remains attached up to a very late period on the point where the pollen-tube entered, which can always be recognised by the three to five contiguous cells appearing brownish as if dead. Two extremities may be distinguished in the part of the pollen-tube which has entered: the upper closed end, which went first in the act of penetration (fig. 150. *y*); and the other, which loses itself externally in the pollen-granule (fig. 150. *x*). The former is firmly applied upon the layer of cells investing the embryo-sac; it may be called the stem end, and the other the root end. In the rest of its periphery the pollen-tube, and therefore the embryo, remains quite free. Close beside the stem end, immediately at the point where its connection with the cellular layer of the nuclear papilla ceases, is now developed the bud (figs. 149. *D*, *f*, 150. *b*), which may here be regarded as a first lateral bud, an axillary bud of the first leaf (figs. 149. *D*, *g*, 150. *d*), or coty-

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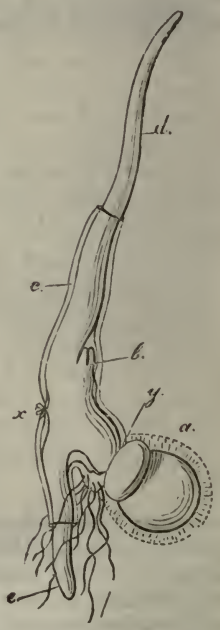


* On the Germination of *Pilularia globulifera*, in the Flora, 1840, No. xxxv. p. 545. (Otherwise an excellent treatise, with many very accurate observations.)

† Ann. des Sc. Nat. 1837, April, p. 221.

‡ Wiegmann's Archiv, 1838, vol. ii. p. 82.

150 *Pilularia globulifera*. A considerably advanced stage of development. *a*, Seed-bud; *b*, axillary bud of the embryo; *c*, the nucleus, expanded into a sheath for the embryo; *d*, first leaf; *e*, first root; *x*, pollen-tube; *y*, collar-like thickening of the coriaceous coat.

ledon, since the proper terminal bud does not become developed on account of its intimate connection with that cellular layer investing the embryo-sac, already alluded to. The difficulty of drawing this parallel in the discoid cotyledon of *Salvinia* is only apparent, if we take the cotyledon of *Lemna*, for instance, as the basis of the comparison. The first lateral bud growing forth then forms a horizontally advancing stem, a rhizome (*rhizoma*), wholly agreeing with so many *Phanerogamia*, as, for example, *Asparagus*. In *Salvinia* no further development of the radical extremity occurs, but in *Pilularia* a root (fig. 150. *e*), which is to be regarded as an adventitious root, is always produced on the side of the stem, exactly opposite the bud, immediately beside the firmly attached radical point.

§ 117. On the full-grown plant are formed, from the lower part of the leaf-stalk (in *Marsilea quadrifolia*), or at its base (*Marsilea pubescens*, *Pilularia*), little nodules, which subsequently grow out into a fruit, borne upon a stalk, which is sometimes long, sometimes short, or (as in *Salvinia*) a little branch springs from the base of the leaf-stalk, hangs down in the water, and produces a number of little fruits arranged upon it in the form of a spike.

The fruit of *Marsilea* is nearly ovate, compressed on two sides. A tough, coriaceous coat, subsequently opening in two valves, surrounds a cavity which is divided into two chambers by a longitudinal septum, imperfect at the upper part, and each of these compartments is again divided by transverse septa into from five to twelve chambers. From the region of the point of attachment of the fruit, on the upper side, where the longitudinal septum is wanting, runs a cord of gelatinous cellular tissue, wholly free except at that point of attachment, which bears on each side from five to twelve little sacs, also composed of gelatinous cellular tissue, and hanging down in these lateral chambers. Through these sacs, almost entirely on the outer side, runs a cord of dense, but also gelatinous, cellular tissue; and the two kinds of reproductive organs are attached to this in such a manner that the seed-sacs, fewer in number, only occupy the more central portion, that next the longitudinal septum. The stalked seed-sacs so enclose the already described seed-buds that the nucleus is turned toward the stalk; they subsequently dehisce. The anthers are irregular, pyriform sacs, containing a great number of pollen-granules, which are composed of a pollen-cell, external pollen-membrane, and in addition to these a special gelatinous coat.

The fruit of *Pilularia* is globular. The equally tough, coriaceous coat, subsequently dehiscing in four valves, surrounds a cavity which is divided into four chambers by vertical septa. In the middle of the outer wall of each chamber runs a cord of gelatinous cellular tissue, which bears the anthers and seed-sacs on its inner side. The latter are distinguished from those of *Marsilea* by the nucleus lying on the side opposite to the stalk. Here, also, the seed sac dehisces, and allows the seed-bud to escape. The anthers are like those of *Marsilea*, but the pollen-grains want the gela-

tinous envelope, while their external pollen-membrane is tough and studded with papillæ.

In *Salvinia* the seed-buds and anthers are in distinct fruits. On each spike is to be found an upper fruit, somewhat removed from the rest which are crowded together, and this alone contains seed-buds. The fruits are vertically furrowed, like a melon, and in each projecting ridge runs an air-passage, again divided by a horizontal septum; otherwise, the cellular tissue surrounding the cavity has delicate walls, and becomes gradually dissolved without any regular dehiscence of the fruit. Into the cavity of the fruit projects, from the base to about half-way up, a central columella, spherically expanded above, which bears upon its globular end in one kind of fruit the seed-sacs, in the other the anthers. The peduncle of the ovate seed-sacs is composed of several collateral rows of cells. The sac (a single layer of cells) encloses the seed-bud (the nucleus of which lies as in *Pilularia*), and separates with the seed-bud from the peduncle. The peduncle of the globular anthers consists of a single row of cells. The external pollen-membrane is very thin and smooth.

*Azolla* is not, I believe, nearly sufficiently investigated; what has hitherto been found allows of no reference to the analogous organs in the *Rhizocarpeæ* above mentioned. I myself have not been able to examine any yet, and I refer to Robert Brown* and Meyen† for more special details.

For the illustration I give the analysis of the reproductive organs of *Salvinia natans* (figs. 151, 152.). The course of development of the

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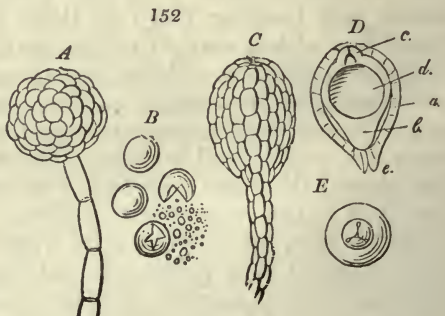


* Verm. Schrift. vol. iii. p. 22., and vol. i. p. 162.; and the Atlas of Flinders's Voyage, which contain Ferd. Bauer's beautiful illustrations.

† Acta Ac. C. L. N. C. vol. xviii. part i. p. 508.

151 *Salvinia natans.* Portion of a flowering plant, with two leaves, a branch dipping down in the water, from which a tuft of rootlets springs, and which bears at the lower part capsules with pollen-sacs (anthers), and above, somewhat removed from the rest, a solitary capsule (*a*), which bears seed-sacs.

152 *Salvinia natans.* *A*, Pollen-sac. *B*, Pollen-granules; two compressed, with their

fruit, which promises results in the highest degree interesting, is up to this time a *pium desiderium*. The *Rhizocarpeæ* have found no place in Meyen's *System* (!). From what is known, and what I have myself seen, this much follows, that there is no room at present for fictions of blending together of organs and the like. On the other hand, from the situation of most of these fruits (comparing them with the *Lycopodiaceæ*), it is exceedingly probable that we have to do merely with a small portion of a leaf, developed in such varied ways in its interior. But this does not at all give a different import to the anthers and seed-buds from that universally admitted for sexual plants; and the fact that in the *Phanerogamia* the anther only is formed from a leaf, the seed-bud probably only from a stem, is thus peculiar to this group, but by no means an essential part of the conception of anther and seed-bud. To attach in this way to every word an absolute definition, and not to use it to express misty schemata of the imagination, is the only way to bring security and progress into science, and to free it from the nauseous and not merely fruitless, but terribly destructive, indiscriminate use of words by which no two persons understand the same thing. The process of development appears to be especially peculiar in the seed-buds of *Pilularia*. In some earlier conditions of these I found the seed-sacs filled partly with delicate transparent globular cells, and partly with groups of four tetraedrally-united cells; one of the latter gradually underwent considerable expansion, but especially in *one group* which occupied exactly the centre of the seed-sac, so that this soon filled the greater part of the space, and could no longer be mistaken for anything else than the future embryo-sac. All the rest of the cellular tissue appeared to be subsequently converted into the coriaceous coat of the embryo-sac, and the gelatinous one of the seed-bud; but my observations on this point are imperfect.

I have thus largely treated of the *Rhizocarpeæ*, only because in no previous publications have the so desirable completeness and accuracy been attained, and in the belief that I was able to furnish some not unimportant contributions; besides, also, that their position, as a decided intermediate link between the *Phanerogamia* and *Cryptogamia*, makes an accurate knowledge of them in the highest degree important and fruitful.

§ 118. The structure of the *Rhizocarpeæ* is, on the whole, very simple. The stem consists of a central vascular bundle, with some spiral vessels, and a bark in which run a circle of large air-canals, covered on the outer side by a simple layer of cells (in *Salvinia*), or by several layers (in *Pilularia* and *Marsilea*). The septa of the air-passages of the last consist of elegant stellate cells; in both *Pilularia* and *Marsilea* the vascular bundle is enclosed by a simple layer of elongated parenchymatous cells with brownish walls. The leaf of *Pilularia*, and the petiole of *Marsilea*, are formed exactly in the same way as the stem of *Salvinia*, only they are, in addition, covered by an epidermis with stomates. The blade of the leaf of

contents. *C*, Seed-sac. *D*, The same in longitudinal section: *a*, seed-sac; *b*, coriaceous coat of the seed-bud; *c*, three-lobed coat of the seed-bud surrounding the nucleus; *d*, embryo-sac; *e*, the place where the pedicle of the seed-sac was attached. *E*, Apex of the seed-bud, seen from above.

*Salvinia* consists of an upper, under, and central layer of cells, which are somewhat removed from each other, the space between them being divided into large air-cavities by vertical septa, the cells of which exhibit undulating walls. The upper layer consists of polygonal cells, which have intercellular passages (stomates) between them, opening into the air-cavities beneath. The upper surface is also studded with tufts of hairs, composed of cells in a moniliform arrangement; the lower surface of the leaves, the stem and the radical fibres, are covered with hairs of a somewhat different kind, composed of cylindrical cells arranged into filaments, the last cell of which is apiculate, and contains some dark-coloured substance. The blade of the leaf of *Marsilea* consists (according to Bischoff) of parenchyma, traversed by forked, branching vascular bundles, and covered by an epidermis furnished with stomates on both (?) surfaces, and having the lateral walls of its cells serpentine. The coriaceous coat of the fruit in *Marsilea* and *Pilularia* is composed of from three to five layers of cells, elongated vertically to the surface, of various colours, unequal in width, but all with thick walls; in *Pilularia* this is immediately invested on the inner side by a brownish parenchyma, composed of small cells, and forming air-cavities in the places between the fruit and the septum; next to this (and *exclusively* in *Marsilea*) by a layer of gelatinous cells, which in *Marsilea exclusively* form the transverse septa, while in *Pilularia* a double layer of thick, brown, minute-celled parenchyma also traverses these. The longitudinal septum, also, in *Marsilea* consists of gelatinous parenchyma. At its upper free border, from the base of the fruit outward, runs a vascular bundle, which sends off as many main branches as there are transverse septa, and these main branches, divided by bifurcation about the middle and then at the very bottom, form a complicated anastomosis. Of the outermost of the very minute cells of the coriaceous coat of the seed-bud in *Pilularia*, those situated in the half lying next the nucleus are somewhat more elongated, so that they form a collar round the seed-bud. In *Marsilea*, the exterior cells are elongated perpendicularly to the surface, yellow, and pass immediately into the cellular integument.

The history of development of the various masses of gelatinous cellular tissue, which appear so peculiar in many respects, still remains an especial desideratum. The cellular cord, bearing little sacs, which in *Marsilea* lies in the fruit, not more than two or three lines long, expands after the dehiscence of the fruit, through absorption of moisture, to the enormous size of a round filament from one to two lines thick, and four to five inches long, the volume exceeding twenty or thirty times that of the whole fruit. The layer of gelatinous cells, which enclose the seed-buds in *Marsilea* and *Pilularia*, is also peculiar, and undergoes continual change during the development, from the action of the water absorbed. Many other specialities are to be found in Bischoff. *

* Kryptogamische Gewächse, p. 72, et seq.

### b. *Plantæ thalamicæ.*

§ 119. Three especial points separate the *Phanerogamia* from the *Rhizocarpeæ*, which approximate so closely to them in the most essential conditions. First, the course of development of the young plant; since the seed-bud (ovule) is penetrated by the pollen-tube while still organically connected with the parent plant, and this end of the pollen-tube, endowed with a capability of development, takes the form of a rudimentary plant; the embryo, which, suddenly arrested in its growth, separates with the seed-bud (now called the seed) from the parent, and then, after some time, throws off its envelopes and unfolds itself (germinates) into a perfect plant. Secondly, the fact that the physiological difference of the two organs, seed-bud and anther, is here also connected with the morphological opposition of stem and leaf. Thirdly, the organs of reproduction are here again enclosed (as in the Mosses and Liverworts, only under more definite conditions) by a number of peculiarly modified leaves forming the flower (*flos*).

Reviewing, under the guidance of what has been stated in the foregoing pages, the whole series of stages by which Nature works her way up to the *Phanerogamia*, if we banish all baseless dreams and flights of fancy, as unscientific, and hold simply to the product of unprejudiced observation, the following conclusions become evident: —

1. The cell is the simple element; it is the whole plant, without organs, and uniting in itself all physiological forces. *a.* Gradually, in portions of it, or in the next stage where several cells are combined, though as yet in exceedingly indeterminate forms, in entire individual cells, we note the appearance of organs (*sporangia*) which are especially devoted to the formation of reproductive cells, the spores. *b.* The form of the cells combining to constitute a plant remains still undefined, but several of these *sporangia* combine in a definite form as a sporocarp; and, lastly, *c*, in the Lichens the spore becomes perfected as an independant organ, by the addition of a special coat. (The *Charæ* remain still inexplicable).

2. Nature advances, causing the cells to combine into determinate, fixed, elementary forms, in fact, into stem and leaf, at the same time retaining the sporocarp, which developes in its highest complexity, and essaying the formation of a new organ essentially consisting of a large cell enclosed in an ovate, cellular body, to which at this stage no definite function is delegated. Neither this nor the sporocarp stands in definite relation to stem and leaf (but there are still important deficiencies in our observations). Lastly, the sporocarp and that other organ become surrounded by leaves, which are modified in definite gradations, forming a flower (Mosses and Liverworts).

3. Through the *Lycopodiaceæ*, Ferns, and *Equisetaceæ*, the sporocarp becomes continually more definitely connected with the leaf, and the development of the sporophyll (spore-leaf) into a peculiar modification (the anther of the *Phanerogamia*) progressively more clearly marked. In its highest condition in the *Equisetaceæ*, the physiological opposition of leaf

and stem, which had been completely unfolded in the *Lycopodiaceæ* and Ferns, appears to retreat again. In *Equisetaceæ* and *Lycopodiaceæ*, nature apparently drops for a time that second organ mentioned in the Mosses; here, however, there is again great want of observed facts.

4. This is again taken up in the *Rhizocarpeæ*, and a definite physiological function attached to it; it becomes the seed-bud (ovule), and the sporocarp the anther; leaf and stem remain as morphologically and physiologically distinct organs, without, however, the reproductive organs being determinately divided between them (but here, again, there is great want of investigation).

5. Lastly, in the *Phanerogamia* nature again takes up all the separate, successively evolved and gradually completed elements, and combines them into a perfect plant. Leaf and stem, morphologically and, in general, physiologically separated, form the entire plant. The stem is developed at certain points into perfect seed-buds with definite function; the leaf, in like manner, into perfect anthers; and both become enclosed in definitely modified leaves, and constitute perfect flowers. Now, however, but with a constant retention of the *essential*, a wide field is opened for the development of the separate parts into varied forms, under which circumstances even particular earlier stages of individual organs reappear; for instance, the leafless stem, flat in *Lemna*, solid in *Melocactus;* the sporophyll of the Ferns in the *Cycadaceæ*, perhaps even the development of the anther out of a stem-organ (?) in *Caulinia fragilis*, the stem of an *Equisetum* with the function of a leaf in *Casuarina*, *Ephedra*, *Cacteæ*, &c. *

I have here only insisted on the main points, in order that the survey might be more easy, but there are many others which might be traced out in the same manner. In the Mosses, for example, the stem originates as an organ morphologically bounded at one extremity; in the Ferns, &c., morphologically limited in two directions, as stem (*sensu stricto*) and root; but in neither exists any relation with the two ends of the spore-tube. This relation first appears in the *Rhizocarpeæ*, and in the *Phanerogamia* it becomes so perfected that the stem, without exception, originates from the penetrating, closed end of the pollen-tube, and the root from the opposite extremity.

For the rest, I leave the special establishment of what has been stated in the paragraphs to the succeeding pages, only remarking, once more, that all that is said about stem and leaf, so far as it agrees with what has been previously mentioned, holds good also of the rest of the *Gymnosporæ*.

* I here expressly beg that no one will impute to me the folly of imagining that, in what I have just said, I have cast a peculiarly profound glance into the mysterious workshop of Nature, that I might, as indeed often happens in our days, by such an assumption of wisdom establish a vain system which investigation would, perhaps, to-morrow cast aside as rubbish. I have only adopted the means which, with our human finite minds, we so often have recourse to in endeavouring to facilitate the survey of the whole series of forms by a figurative representation. I am defended against the danger of regarding it as anything more, by the healthy plainness which I owe to my teacher Fries, from whose logic I have learned as much Botany as from all botanical treatises put together.

## X. XI. MONOCOTYLEDONS AND DICOTYLEDONS.

§ 120. In the development of the pollen-tube into the embryo, an essential distinction arises, according as there is formed *one* first leaf (*cotyledon*) growing up from the whole circumference of the rudimentary stem, or *two or more* first leaves, which collectively embrace the stem, all on the same level. On this depends the distinction of Monocotyledons and Di- or Polycotyledons, with which is connected many other essential peculiarities; for instance, that of the closed vascular bundles which are peculiar to the former, and the unlimited bundles of the latter. Since, however, the distinction of the two groups can only be established in so few parts at this stage of our inquiries, it is better, to avoid repetition, to treat both together as *Phanerogamia*, in the order of their individual organs.

With all its correctness, I hold the division of the *Phanerogamia* into Monocotyledons and Dicotyledons to be but provisional. A perfect morphological system will certainly first necessitate the distinction of *Gymnosperms* and *Angiosperms*. The former without germens (and mostly with homogeneous wood), comprehending the *Coniferæ*, *Cycadaceæ*, *Loranthaceæ*, and *Gnetaceæ* (?); the latter with the young fruit in the form of a germen (and mostly heterogenous wood), separating into Monocotyledons and Dicotyledons. At present, however, our knowledge, so generally imperfect in reference to the majority of points connected with the course of development, does not allow of this division being established and carried out with any completeness.

§ 121. It will be universally admitted, that in its formation, every Phanerogamous embryo attains to a stage in which it appears within the cavity of the seed-bud as a little round or ovate body, homogeneously composed of cells, and in which distinctions neither of organ nor structure are to be discriminated. To start from this condition, as a perfectly certain element, is sufficient, but it is necessary to go back quite to this point to acquire a comprehension of the fully formed embryo and the entire plant. This little body forms all the cells, through which it grows and developes, *inside* its own proper boundaries; no organic parts are added from without; it is, therefore, the entire plant in its simplest rudiment. The central portion first ceases to produce new cells; below (where the pollen-tube penetrated the seed bud) and above (the point opposite the former) the formation of cells, and with it the development, proceeds, but in various ways and naturally opposite directions. Below (the radical extremity) the embryo elongates into a more or less conical point, the radicle (*radicula*). Above (the cauline extremity) we find the following: the apex elongates in a direction opposed to the rootlet, by the formation of new cells, in such a manner that part of the new cells are constantly applied upon the old ones, while part recompose the extreme point as formative cells. At a variable distance below the apex there is a

region where new cells are also formed, but so that the new ones are partly pushed outwards and partly persist as formative cells in the vicinity of the stem. In this way a mass of cellular tissue is expanded out in the form of a lamina from this region of the stem, appearing either as an undivided organ continuous in its whole circuit at the base, or, divided from the very bottom into two or more portions, it presents itself under the form of two or more organs all situated in the same plane. Through the accumulation of cells upon the elongating apex, the lateral region just described is removed continually further from the peculiar throng of active cell-formation; perhaps it is on this account that its formative power is exhausted after a certain time. The further enlargement of its organs depends then solely on the expansion of cells already formed, but this also has its limits. Thus, we find here two essentially different form-producing processes, and we call their products elementary organs of the plant: Stem (*caulis, sensu stricto*) the product of the first, formative force originally acting continuously and unlimitedly in one direction; Leaf (*folium*) the product of the second, dependent force, which defines its own boundaries in the manner peculiar to it. The first leaf or first leaves are called *cotyledons*. If we refer the term to a line * drawn from the root-end through the middle of the embryo to the stem-end, which then answers at once to the direction of development both of rootlet and stem, the stem is called an axial structure (*axis*), the leaves lateral organs (*partes laterales, appendiculares*). In most cases, some more succeeding leaves, besides the cotyledons, are formed on the embryo; these, with the rudimentary stem on which they are borne, are called the plumule (*plumula*). Then ensues a pause in the formative activity, the embryo is finished, the seed (the seed-bud surrounding it) is ripe.

In all common plants the root, stem, and leaves are so conspicuous, that their distinction in language is much older than any trace of a scientific contemplation of plants. At the same time, nothing has so entangled science, for a long time deprived it of all secure foundations, as those very three organs; and for this reason: that men were contented to transfer these into science as they were intuitively understood in common life, and neglected to transform the obscure notions of the sensuous perception, which vary with the mode in which an impression is received in every individual, and are, therefore, wholly incommunicable, into a clear definite conception framed from their characteristics, and therefore universally communicable. DeCandolle begins: "*Les feuilles sont*, COMME CHACUN SAIT, *les expansions ordinairement planes*," &c. What, then, is a science for, if it brings us nothing more than what every one knows without it? One cannot dispute at all with most botanists whether anything is a leaf or not, because they do not seek in any way to explain in what its characteristics are to consist, as, for instance, Agardh, DeCandolle, Link, and others. The greater portion throw in some character or other, which the most superficial knowledge

* Which may also be a curved line, from the action of external influences.

points out to be insufficient, and that is all very well; for instance, the flat expansion, the bud in the axil, the respiratory function, and so on. With the statement of that which leaves "*ordinairement*" are, nothing at all is done; in science we have precisely to insist on what is necessary and constant. For the stem, in opposition to leaf and root, again, most authors have no definition whatever; or it is so fragmentary, that a very moderate acquaintance with plants causes it to be cast aside, for instance: The stem is the portion striving upwards, the axis of the plant (Kunth). What, then, is the horizontally advancing rhizome of *Asparagus*, what the flowering stem of *Arachis hypogæa*, nay, what even the twig of the Weeping Ash? (It is similar with Lindley, Link, and others.) Agardh defines: The stem is that part of a vegetable from which the leaves *appear* to issue, and which *appears* to grow upward. That no scientific definition can be built on mere *appearances*, every one will understand who has not renounced all sound logic; but what is the stem of *Melocactus*, from which leaves neither issue nor appear to do so. But enough of these examples. This much is clear, that we require, in science, more definite and unchangeable characters, to keep apart the conceptions which we wish to separate as actually different; and, on the other hand, such general characters that no member which belongs to the sphere of the conception shall be excluded from it. By accurate and comprehensive investigations of nature, we are led to those distinct oppositions of radicle and axis, of axis and leaf. The latter contrast is actually manifested in nature; whether it is to the purpose to attach chosen words to it, is another question. The former contrast, as primary and original in the development, preeminently deserves an especial name, and in this way every one knows certainly what he has to deal with, when leaf, axis, radicle, &c., are spoken of; and it is precisely on this that all possibility of scientific intercommunication and progress depends. The history of the formation of the embryo given above, which it may be observed was known in its principal points long ago, nay, which is to be found truly even in Malpighi *, refutes sufficiently all empty fictions as to the origin of the axis from combined leaf-stalks. Nature first displays a little undivided body (fig. 153. *a*), which immediately elongating upwards becomes axis, and downwards radicle. The forms which we have named leaves (fig. 153. *b*, *c*) issue out of this axis which pre-existed: and that fiction is to the effect of nothing less than to describe the origin of an existing thing out of the blending together of two things which have no existence. Nay, to cut off all possibility of such flights of fancy, Nature itself had formed the embryo of *Cuscuta*, in which, although it attains a considerable length, no leaves whatever are usually

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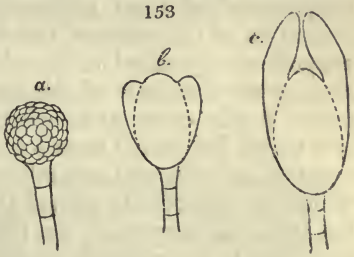


* Anatome Plant., de Seminum Generatione, pl. xl. fig. 242. in Pisorum semine.

[153] *Hypochæris radicata.* Development of the embryo. *a*, Youngest condition: the embryo attached upon the suspensor, composed of three cells, is a little globule formed of cells. *b*, Somewhat older germ: the dotted line indicates the original body, from which the two first leaves (cotyledons) rise upward on each side of the apex (terminal bud), which remains free. *c*, The same, but in a more advanced stage.

found in the embryonic life, and only little scale-like ones at a very late period after germination.

The different modifications of the form of the embryo and its parts will be treated of subsequently when speaking of the seed. Here it was only dealt with in order to become acquainted with so much of the course of development as appeared necessary to the comprehension and the establishment of what follows. Indeed, it is always dangerous to interfere in the current of organic development and to define the commencement. Are we to begin with the egg because the hen originates from it, or with the hen because she lays the egg? Great circumspection is necessary to arrive at the simplest point of departure, and repetitions are unavoidable, since, in order to completeness, we must make the circle of development return again into itself.

§ 122. After a variable period of rest, the development of the embryo into a plant (germination) commences, upon which it throws off the coats of the seed enclosing it. The same process which effected the perfect formation of the embryo now recommences; the radicle elongates into the root and forms branches, and the axis elongates in its appointed manner, and at the same time continuously pushes forth leaves. Thus originates the simple Phanerogamous plant. The axis and leaves, however, gradually assume, through different forms and conditions of position, a different morphological import, until their power of development is exhausted by the formation of a new individual, and ceases. From the axis are frequently developed, in a way very different from the formation of the radicle and its ramifications, organs which, on account of their many essential agreements with true roots, we call *adventitious roots* (*radices adventitiæ*). But the plant seldom or never remains simple; in the angles which the leaves make with the upper internodes, the axils of the leaves, fresh processes of cell-formation originate which form rudimentary axes and leaves, repeating the formation of the embryo, but without radical extremities, and these are collectively called *axillary buds*. Under certain circumstances, also, new individuals of this kind originate on the axis, *scattered buds;* finally every axis, whether it be that of a simple plant, or one which has issued from a bud, naturally terminates in the rudiment of an axis, and a number of more or less rudimentary leaves, which are collectively named the *terminal bud*. Thus we obtain the following survey of the portions of the plant, which must be individually more closely examined: —

*A.* Radical organs.

1. The radicle and its development. 2. The adventitious roots.

*B.* Axial organs.

1. The axis and its development. 2. The receptacle, the disc. 3. The placenta. 4. The seed bud. 5. The seed.

*C.* Foliar organs.

1. The leaf. 2. The floral envelopes. 3. The stamen. 4. The carpel. 5. The fruit.

*D.* Gemmal organs.

1. The bud. 2. The horizontal axis. 3. The inflorescence. 4. The fruit-stalk.

*E.* The new individual, the embryo.

In the following pages I shall alter the arrangement a little, for the sake of convenience. It suffices to have here summarily noted the systematic arrangement deduced from the nature of the plant.

I know well that it is more to the purpose, enables us to avoid repetition, and renders the comprehension more easy, to treat of the plant, at least the essential particulars, according to the established plan: root, stem, leaf, flower, and fruit. But there is an important error in all our manuals, in that the complicated organs like flower and fruit, the derived organs like rhizome, inflorescence, &c., are either not at all traced back to the elementary organs, or what their nature may be is mentioned so briefly under each particular head, that any clear survey of the whole plant becomes impossible to the learner. But a correct insight into the nature of the Phanerogamous plant can only be gained by placing the reduction of all the separate parts to the two only kinds of elementary organs, the axis and the lateral bodies, at the commencement of the whole inquiry, so that the reference to these may accompany us into the investigation of each individual part.

For the rest, the parts distinguished are, perhaps, in some cases mistakenly separated; in others, perhaps, the essential differences are not all completely kept asunder, indications enough of which will occur in the subsequent descriptions. I therefore neither consider myself authorised, nor at present able, to carry out a consequent natural division, and to propound the wholly new terminology which this would require; nor do I believe that, in the present condition of science, any essential improvement would be effected by such a step, since so many and so important matters still remain unsettled, and therefore, instead of a fundamental re-formation, a mere piece of patchwork would be the result. Where I think corrections necessary, I will note them under the particular heads.

## A. Radical Organs.

### a. *True Root* (Radix).

§ 123. In germination, the process of cell-formation mostly recommences in the radicle of the embryo, in such a manner that the outermost layer of cells of the extreme point of the root remains unaltered, while the process of development begins immediately beneath this; continuous portions of the newly produced cells, subsequently forming no fresh cells, become deposited toward the base of the root, and other portions continue the process of development immediately under the apex of the radicle, so that the base and the extreme point contain the oldest cells; the apex becomes pushed forward, and the youngest, and therefore most delicate, cells are always situated immediately beneath it: in this way the radicle of the embryo is developed into the root of the plant.

*Epiblema* and vascular bundles are formed in the root in the manner already described; the latter are so placed that they present a closed circle in the cross-section. In Monocotyledons they are closed or *definite* bundles; in Dicotyledons *indefinite.* They enclose a minute pith. Liber-bundles, milk-reservoirs, and milk-vessels are sometimes formed in the bark.

The distinction between main root in the immediate elongation of the radicle, and branches of the root which issue from that subsequently, is the only one morphologically essential; on the other hand, it is necessary, in a physiological point of view, as will be discussed hereafter, to distinguish the simple, newest, and still advancing end, from all other parts of the radical system.

That every true root has a distinct, even though minute, pith, i. e. a parenchyma enclosed by a circle of vascular bundles, is demonstrated by every longitudinal and transverse section brought beneath the microscope.

b. *Adventitious Root* (Radix adventitia).

§ 124. Adventitious roots are developed, in a peculiar manner, from the axis, either under favouring external conditions (as, for instance, a considerable degree of moisture, artificially as in cuttings, naturally through the weak axis lying upon the ground as in the so-called *runners*); or with specific regularity, as in Grasses, plants with aërial roots, &c., and from the true root, but here in perfect regularity. In the bark, close upon the vascular bundles, originates a little conical group of formative cells, which separates quite down to the base of the cone from the surrounding cells, and, taking on the process of growth peculiar to the root, breaks a way for itself through the bark and becomes free. In this act it usually compresses that portion of the cortical parenchyma lying in front of it; this dies, is torn away, and often remains adherent for a long time upon the apex of the root as a little cap, as, for instance, in *Equisetum*, *Pandanus* *, &c. This must not be confounded with the calyptra of the root on the adventitious roots of plants rooting in water, such as *Lemna* †, *Pistia*, &c.

In most of the tropical *Orchideæ*, in many species of *Pothos*, the adventitious roots, which may be developed either in the air or in the ground, have a peculiar investment over their true epidermis (§ 29.). These appear to deserve a special name, and I call them coated roots (*radices velatæ*).

When the adventitious roots are produced regularly upon those internodes of a species of plant exposed to the air, they are named (with a superfluous term) aërial roots (*radices aëreæ*).

* According to DeCandolle, Organographie Végétale, vol. ii. pl. 10. I have never seen it in our hothouses.

† Here we have a striking example of how senseless the terminology sometimes is. The roots, hanging perpendicularly down in the water, of the floating *Lemna* are named *radices natantes.* One might just as well talk of a swimming anchor, which, with thirty fathoms of cable, does not yet reach the bottom. Such things never happen to plain every-day people, only to a scholar who has wholly destroyed his healthy powers of perception by book-wisdom and an in-door life.

All rooting of an axis of a bud, except that of the embryo, occurs by adventitious roots. The region just below the base of a leaf appears to be most inclined to the production of roots.

In the formation of an adventitious root, a vascular bundle is developed in it, issuing from the vascular bundle of the stem.

Only in very few manuals do we find a merely indicated, in none a strictly and consequently traced, distinction between roots and adventitious roots, which are so thoroughly different in their course of development and morphological import. Theories of the function of the root, Vegetable Systems founded on the structure of the root, endless contests about nutrition, the distinction between Monocotyledons and Dicotyledons, &c., in short, a whole literature owes its origin solely to the neglect of this essential distinction. In the Monocotyledons it often readily happens that the adventitious roots are *exclusively* observed, and this led Richard to divide plants into *Endorhizæ* (with roots which break through from the interior, Monocotyledons), and *Exorhizæ* (the roots of which are formed by the mere elongation of the radicle, Dicotyledons). Dutrochet, who observed the formation of adventitious roots on a Dicotyledonous rhizome (stem), opposed, at once, that all plants are endorhizous. Both are wrong. DeCandolle discovered the cap upon the adventitious roots of *Pandanus*, and we had directly a great theory about the spongioles (*spongiolæ radicales*), bodies which have no existence; and those caps, the cap of the root of aquatic plants and of common root-ends, were all thrown together under this head. Had half the time which has been wasted in the spinning out of such untenable and useless hypotheses been applied to fundamental investigations, in what a different position would Science stand!

In most plants of which the radicle does not become developed, for instance, most Grasses, *Lemna*, &c., the course of formation of adventitious roots may be traced completely even in the embryo; more will be said on this point under the head of the seed. For the others, the rhizome of *Phragmites communis* and *Nymphæa alba* are to be recommended. A peculiar structure, the physiological import of which is still very obscure, the cap of the root (*pileorhiza*), occurs in the *Lemnaceæ* (fig. 154—156.), *Pistiaceæ*, and some other water-plants, e. g. *Hy-*

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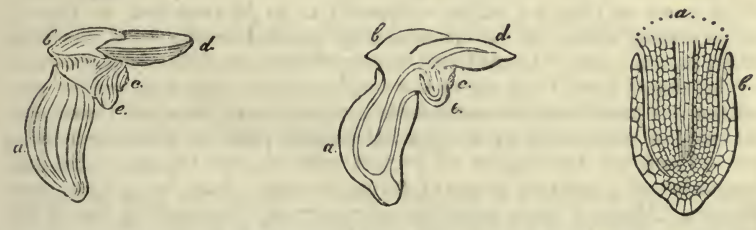


[154] *Telmatophace gibba.* Embryo: *a*, the seed; *b*, the cotyledonary mass; *c*, the radical end, with its covercle (*embryotega*, Gaertner); *d*, the bud breaking forth from the transverse slit of the cotyledon; *e*, protuberance which precedes the issue of an adventitious root.

[155] Longitudinal section of the preceding. In the seed (*a*) may be distinguished the testa, a thin endosperm, and the cotyledon, in the middle of which runs a vascular bundle, which gives off one twig to the bud (*d*), and another to the adventitious root (*e*). In the latter, the cap may be distinguished from the root itself.

[156] *T. gibba.* The adventitious root from fig. 155. in longitudinal section, strongly

*drocharis Morsus ranæ*, according to Meyen. Simultaneously with the origin of the root under the bark (fig. 155. *e*), a cellular layer (fig. 156. *b*), completely enveloping the little cone constituting the root, quite down to its base, separates wholly from the cortical parenchyma in these plants, still, however, retaining its vitality, and in vital connection with the extreme point of the root; the cellular tissue of the apex of the root, and that of the cap of the root, always passing into one another here. Under natural conditions, this cap of the root is persistent during the whole life of the root, but if torn off it is never reproduced, and the root dies.

In some parasites, e. g, in *Cuscuta*, and also frequently in *Hedera*, the bark swells out into a disc (sucker, *haustorium*) over the developing adventitious root, and this, originally applied flat upon the foreign body, subsequently becomes concave, from the especial extension of its border, and (exactly as in the sucking-disc of the leech, or the pro-legs of caterpillars) attaches the parasite to the support by a vacuum. From the bottom of this disc springs the adventitious root, which, if it proceeds forward, penetrates the supporting body.

Comprehensive comparative researches into the anatomical structure of adventitious roots are still a desideratum. The only accurate ones we at present possess are from Mohl * and Mirbel † on the Palms.

§ 125. The varieties of form in true and adventitious roots are not very manifold, and they depend on their *direction, arrangement*, as well in regard to the stem as among themselves, preponderating *formation of parenchyma* in particular places, and formation of wood, through the indefinite vascular bundles of the Dicotyledons. No root is capable of producing buds. In a large portion of the Monocotyledons, especially in the Grasses, and all those in which the seed is furnished with an operculum (see, hereafter, under the head of the Seed), even in some Dicotyledons, for instance, *Nelumbium*, the radicle is not all developed in germination. Consequently, these have no true root; in place of this, adventitious roots are immediately formed (see the preceding paragraph).

All botanists fully agree, that everything developed from the plumule and buds, above the cotyledons (leaves, and the readily distinguishable aërial roots, as they are called, excepted), is to be reckoned as part of the ascending axis; but at one time they counted among roots, the bulb, tuber, rhizome, many-headed root, premorse root, &c., clearly parts which are developed from buds above the cotyledons; or raised an endless contention, on manifestly unsustainable ground, as to whether these parts are roots or not: certainly a right substantial proof of what perversities are induced by the neglect of correct method, and the one-sided contemplation of a solitary stage of formation torn from its normal connexions. Most of these forms are now correctly disposed of, but a few botanists still hold to a part of the old beaten path.‡

* De Structurâ Palmarum. Munich, 1831.

† Nouvelles Notes sur le Cambium, Paris, 1839.

‡ Link (Philos. Botan. edit. 2. vol. i. p. 361.), for instance, still retains the *radix*

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magnified. *a*, The root, in which may be distinguished a central vascular bundle, and a thicker bark. *b*, Layer connected with the apex of the root by persistent cellular tissue, free in the remaining portions.

The direction of the root varies very much, often with specific regularity; but most of what was formerly included here belongs to the axis (in the strict sense). One peculiarity is interesting in its relation to the axis. In the germinating embryo the basis of the root soon becomes a fixed point in the soil, the elongatory root proceeding downward from this, through the earth. In rare cases, in loose mud with a firm substratum, on the other hand, the point of the root very soon becomes the relatively fixed point, from which the elongating root gradually lifts the whole plant upward. This may sometimes be observed in solitary bog-plants. From the descriptions, this is probably the cause, depending upon the locality, of the peculiarity of the so-called Mangrove woods on the shores of the rivers of tropical Africa and America. The peculiar rooting of some Palms, e. g. *Areca oleracea*, in which a number of adventitious roots, springing out almost on one level from the base of the stem, lift up this base a certain height free from the ground and retain it there, depends upon the same cause. The light sandy soil does not give the base of the root hold enough to allow a rapid penetration of the apex into the earth, thence at least part of the elongation only removes its base, and with this also the base of the stem, from the apex, consequently lifts it upward, perhaps till the weight of the stem itself affords a sufficient resistance. One might call it an organic example of the relativeness of all rectilinear motion.

The arrangement of the branches in relation to each other present manifold variation, which, for the most part, depends on the varied position of the branches upon the main root, and their different amount of development.

The preponderating development of parenchyma in certain places produces either mere inequalities of the surface, in the simplest cases papillæ, the so-called radical hairs (fibrils) in moist, loose soils, or considerable expansions above, below, in the middle or throughout the whole length. By the formation of wood, the root of the Dicotyledons comes wholly to resemble the stem; I will give the necessary explanations thereupon under that head. This one may well enough name with the otherwise wholly useless term *caudex*.

## B. Axial Organs.

### a. *Of the main Axis* (Axis primarius), *or the Axis of the simple Plant* (*of the second Order*).

§ 126. The axis which is produced from the embryo is called the main axis (axis of the simple plant); those produced from buds, secondary axes.

At the very outset of the consideration of the formation of axes, we must premise that all, according to the specific peculiarity of the plant, live either during one summer only (one period of vegetation, an annual axis), or have a longer duration (perennial axes). The former I especially distinguish by the term stem (*caulis* in the strict sense), the latter I call trunk (*truncus*). The former, again, live only for the

*multiceps* and *præmorsa*, both true stems, among roots. Treviranus (Physiologie, vol i. p. 367.) still treats of bulb and tuber among the roots.

commencement of the vegetative period; or only for the end, e. g. the flower-bearing stalk; or for the whole period of vegetation.

From the embryonic condition forward, leaves are continuously developed at the apex of the axis, and, with minute differences, always closely succeeding one another, so that there is never more than a very short portion of the axis (internode, *internodium*) between any two contiguous leaves. But the cells composing this internode frequently continue for a short time to produce new cells, until enough are formed wholly to perfect the structure of the internode by their mere expansion and further development. By this more complete development, the internode then either becomes elongated, and thus removes the adjoining leaves to a greater distance apart, or this does not take place, and thus the leaves remain stationed immediately above one another. On this depends the *most important of all* morphological distinctions in the axial organs — that between axes with developed and undeveloped internodes. Axes exclusively composed of developed internodes occur, indeed, only among the Dicotyledons. In all axes with undeveloped internodes alone, in all Monocotyledons, and many Dicotyledons, matters are so constituted, that each succeeding internode, instead of becoming elongated, expands in diameter like a disc, and each always to a somewhat greater extent than the preceding, so that thus a sufficiently broad basis is gradually acquired, upon which the axis subsequently rises upward in a cylindrical form by developed or undeveloped internodes. Under these circumstances, however, the base of the terminal bud also naturally grows, and this becomes a cone, of varying length, and of a varying degree of acuteness. In correspondence with this, the undeveloped internodes are usually hollow cones fitting one over another. But they do occur also as true discs, nay, even as discs with a concavity sufficient to render them cup-shaped.

These two forms of the axis, with developed and undeveloped internodes, and both according to their different duration, may alternate repeatedly in the length of the same axis (and still more in the various axes of a plant become compound by development of buds). This composition is completely defined and limited by the habit (*habitus*) in every single species of plant.

At the place where the leaf joins the axis, the node (*nodus*), this frequently exhibits a peculiar expansion or contraction, or both, and these, sometimes below, sometimes above, the base of the leaf, or at others in both situations. This is most frequently met with in developed internodes, especially where the base of the leaf occupies the whole circumference of the axis, or where several leaves share this entirely among them. Various conditions of structure correspond to these external appearances, and the nodes are therefore divided into: perfect nodes, where the peculiarity just described occurs; and imperfect, where it does not exist.

In rare cases a so-called joint or articulation (*articulatio*) is formed, through anatomical conditions, in the situation of the node,

in such a manner that the axis readily breaks off here with smooth fractured surfaces, or separates spontaneously from the plant at a certain epoch, as in many flower or fruit stalks.

Moreover, the observation (§ 68.) formerly made is to be repeated here, that every part of a plant is capable of development in one, two, or three of the dimensions of space; therefore, besides the long and slender, and the short, thick, almost globular, axes, there may be flattened, strap-shaped, or foliaceous stems.

Finally, it must also be remarked here, that there are but very few plants in which the axis is homogeneous throughout, at once in form (as to a certain extent in *Lemna*, which consists solely of one undeveloped internode) and in duration (the few perfectly annual plants excepted, which form neither transitory internodes in germination nor flower-stalks of brief duration at a later period). Most plants have heterogeneous axes, especially of such kind that internodes of different form succeed each other (as in almost every plant), or that the internodes differ in duration (as in the many plants in which the lower internodes form a trunk, while the upper remain as stem).

If we would avoid bringing the greatest difficulty into the study of the stem, we must, throughout, very carefully separate the morphology, strictly so called, from the anatomy.* The mere accident, I might say, that the first Palm-stems were at once studied internally as well as externally, has had much influence in the science. Without any anatomy at all, the trunk of *Dracæna* is essentially distinct from that of *Calamus*, and the distinction is exactly *of the same kind* as that between the trunks of *Mammillaria* and *Æsculus*. Whether and what anatomical differences (besides the general distinction between Mono- and Dicotyledon, which is always premised here) are connected with these essential forms, are questions for subsequent inquiry.

From the division into annual and perennial, into developed and undeveloped, internodes, proceed four forms, of which it is easy to find examples in the vegetable kingdom; e. g. clearly developed internodes, annual *Cannabis*, perennial *Æsculus;* clearly undeveloped internodes, annual *Myosurus* (with the exception of the flower-stalk), perennial *Melocactus*. It would be equally easy to find examples of the combination of these forms in the same plant, nay, even of all possible combinations, which arise if we divide the annual internodes again, as above, into these sections, according to their different duration. The stem of *Avena sativa* frequently commences with a developed, speedily decaying internode; next follow several undeveloped internodes, becoming successively broader; then come again developed internodes.† The two last kinds endure

* As a most striking example of a confusion of ideas, I may here mention that Meyen, in the second division (vol. i. of his Physiology; the first treats of the elementary organs), under the head of "General Comparative Exposition of the Types, according to which the Elementary Organs are combined in the Structure of Plants," treats wholly and solely of the stem; while, from under such a head, one can only think of the study of tissues, organography, natural system, &c.; anything, in fact, but what he gives.

† The same occurs in *Hordeum vulgare*. Apparently it depends, in both, on the position of the grain on the surface of the earth, whether the first internode becomes elongated or not.

through the whole period of vegetation; these are succeeded by the developed internodes of the infloresence, only enduring in the latter part of the vegetative period. In *Zea Mays*, the stem begins with a developed internode, which soon dies; this is succeeded by undeveloped internodes, then developed, both enduring the whole period of vegetation; then follow again the undeveloped ones of the female inflorescence, only existing in the end of the vegetative period. *Chamædorea Schiedeana* begins with undeveloped internodes, then follow developed; both perennial. *Nuphar luteum* begins with a developed internode, which soon dies; then follow undeveloped perennial internodes; then one developed, appearing as a flower-stalk, merely towards the close of the vegetative period. *Lilium candidum* begins with undeveloped internodes which are perennial; then follow annual, developed internodes, &c. These examples might be easily multiplied and completed. Some forms are characteristic of certain groups of plants; for instance, trunks with developed internodes in the *Cupuliferæ*, trunks with developed internodes in the fistular Palms, with undeveloped internodes in the remaining kinds, stem with developed internodes in most of the Grasses, &c. Certain combinations are also characteristic; for instance, perennial undeveloped, with annual developed internodes, in all (?) *Liliaceæ*. But definite forms and combinations are much more frequently found peculiar to single genera or species. Hitherto, far too little regard has been paid to this condition of special regular series of developed and undeveloped internodes in the same axis. The remarkable peculiarity of many genera and species, which, in germination, first form a developed internode, soon decaying again, and succeeded by undeveloped ones, has, in particular, been wholly overlooked. Very different plants furnish examples of this: *Zea Mays*, *Briza maxima*, *Phormium tenax*, *Nymphæa*, *Nuphar*, &c., and at least very frequently *Avena sativa*, and *Hordeum vulgare*. In the axis with undeveloped internodes, frequently, and the oftener when it has commenced by a developed internode, the death of the single joints progresses gradually upward, so that the axis, even when perennial, never attains any considerable length; e. g. in *Iris*, bulbous plants, and most subterraneous axes (*rhizoma*) with undeveloped internodes.

Here, however, I must enter somewhat more minutely into the course of development of these forms of the axis. It has already been mentioned (§ 74.) how every form must be produced solely from the arrangement of the newly developed cells and their subsequent expansion. On this depends all structure of axes. In the embryo, the upper end, from which the axis is developed (the terminal bud), more or less resembles a hemisphere, or a blunt cone. In this part chiefly goes on the formation of new structure, and it always retains its general form. In the axes with undeveloped internodes only, if they expand very much in breadth, does it naturally acquire a larger base, and then becomes, according to its specific peculiarity, either shorter and more blunt (as in most subterraneous axes), or longer and more acute. The process of formation which here takes place has not, indeed, by any means been so accurately investigated as is necessary; but still much may be perceived with tolerable clearness. An eye only moderately accustomed to such matters readily discovers in a plant the situations where an active process of cell-formation is going on, in the *apparently* structureless condition of the yellowish, almost fluid masses (first stage); the situations where the cell-formation has ceased, in the distinct, indeed, but very delicate, cellular tissue (with more homogeneous contents), which

however are still wholly pervaded by sap (second stage); lastly, the cellular tissue, which has already attained a greater age, in the blackish appearance which is produced by the intercellular passages being freed from sap, and containing merely air (third stage). When these points are discriminated, the origin of the forms may be traced pretty easily in most axes.

I. The arrangement of the cellular tissue is effected exclusively in the first stage, and, in all probability, is conditioned:

1. By the arrangement of the secondary cells in the mother-cells. If they mostly lie in a linear arrangement in the long axis of the stem, an elongated internode originates; if they lie mostly towards the angles of a tetraedron, an undeveloped internode; lastly, if they lie chiefly in one plane, this plane may stand at right angles to the axis, and the internodes will be much developed in breadth, or, it may be parallel to the axis, and thus form a stem flattened on two sides.

2. By the form of the process itself, since this ceases in some situations earlier than in others.

*A.* The first distinction to be seized here is that between Monocotyledons and Dicotyledons in general, depending on the division into definite and indefinite, or closed and unlimited, bundles. In the Dicotyledons the process of cell-formation never ceases on the outside of the vascular bundle, whence the individual internodes, so long as they live, continually increase in thickness; while in the Monocotyledons the process of cell-formation 1. ceases regularly from below upward, in the individual vascular bundles, and thus a thickening of the individual internode by their means becomes impossible; but the increase of thickness of the axis itself may be attained by the increasing diameter of the successive internodes (as is shown more fully under *D*), and thence, when it rises perpendicularly in a cylindrical form (if it be such as is represented under *B*, or under *D*), it receives no increase of thickness from that time: or 2. a layer of cells beneath the periphery of the axis retains its capacity of development, and these continually increase the thickness of the axis by their uninterrupted production of new cells, since in the newly-formed tissue vascular bundles are simultaneously continually developed. This process occurs, however, only in the Monocotyledons with undeveloped internodes of a branching type, in *Dracæna*, some Palms (*Cucifera thebaica*), and *Aloineæ*. This second process of formation bears some resemblance to that of the Dicotyledons, in so far that in both a connected layer of cells remains capable of development around the whole periphery. In both, the newly originating cells assume two forms, one portion joining the cellular tissue between the vascular bundles, while another portion belongs to the vascular bundle structure. But the essential distinction remains in this, that this latter portion only increases the existing vascular bundles on the outside in the Dicotyledons, while in the Monocotyledons, on the contrary, it becomes transformed into new isolated bundles.

*B.* If the process of formation progresses regularly from below upwards, while a definite plane of the basis ceases to produce cells, a cylindrical ascending axis is produced. In elongated internodes this is always the case; therefore every internode may be clearly separated from the axis by two cuts.

*C.* If the process of cell-formation ceases somewhat earlier in particular situations in the circumference than in others, the result is the formation of axes with projecting angles; for instance, three-edged,

quadrangular, &c., stems. This condition is most striking when the process of formation ceases very soon on two sides, so that a two-edged stem is thus formed, which very often represents quite a thin plate, and is frequently taken for a leaf, on account of the mistaken notion of regarding the conditions of dimension in space as among the characters of special organs. The best examples are afforded by *Ruscus* and *Phyllanthus*.

*D*. If it endures longer at the circumference than in the middle, the following results present themselves. In the usual conical form of the terminal bud, the process of cell-formation does not in this case occur throughout the whole cone, but only in its outer layers, so that the whole free surface of the cone contains the youngest cells: the whole of the core of the cone is made up of the older. Here the axis usually rises upward in a cylindrical form, not, however, by means of discs equally deposited upon one another (as in *A*), but by hollow cones applied over each other. Every new internode is itself a hollow cone of this kind, and therefore cannot be detached from the axis by a vertical section; it can only be removed by a section following the course of a conical surface. If the process of cell-formation persists somewhat longer in the succeeding internode than in the preceding, a longer hollow cone is produced, which, consequently, stretches out over the base of the former, which should properly be free; and thus the new internode becomes broader in proportion to the former, so much so, that the free borders of the successive internodes, instead of lying in a vertical cylindrical surface, form a horizontal surface (e. g. very often to be observed in *Melocactus*), or, in smaller degrees of projection, lie in a hemispherical surface, having its convexity directed downwards (as, for instance, is seen in most stems which are tolerably thick and enduring, in the first or next succeeding internodes, e. g. in *Zea Mays*, &c.).

*E*. Finally, the forms become most striking where the cell-formation ceases at the border earlier than in the centre; directly the opposite of what occurs in *D*. This seldom happens in a single internode; it is usually found where several very short, undeveloped ones, united together, form but a mere disc. When, for example, a disc or a bluntish cone has originally been formed, and the extreme margin loses the power of development, while the newly forming cells in the middle continue to arrange themselves into a flattened form, the border will at first be capable of yielding to some extent by the expansion of its cells; but this soon ceases, and it must become elevated, while the centre gradually developes itself, into a hollow form, in the same way as a plate of lead becomes hollow when it is beaten out in the middle, and not at the edges. According as the time the process of cell-formation lasts, proceeds quickly or slowly, and according as the arrangement of the newly produced cells is restricted a longer or shorter time to the same plane, does the excavated form become very different. From the quite convex internodes which bear the florets in *Anthemis*, through the flat disc of *Helianthus*, the concave disc of *Dorstenia*, to the longish cup-shaped disk, almost closed above, of *Ficus*, we meet with almost every possible gradation; in like manner we see the same from the convex fruit-bearing internodes of *Potentilla*, through the cup-form in *Rosa*, to those completely closed and blended with the ovaries in *Malus* and *Pyrus*. So that it may be clearly seen, and I here call particular attention to the fact, that, in all these hollow forms, the deepest point in the interior of the cavity corresponds to the terminal shoot; consequently it lies indeed mathematically lower, but organically higher, on the axis than the internal walls of the cavity

and the margin; thus the lowest flowers in the Fig are the youngest, like the innermost in *Helianthus*, the uppermost in *Anthemis:* equally are the lowest carpels in the fruit of the Rose the youngest foliar-organs; the petals and calyx standing on the margin, the oldest. In the same way, lastly, the lowest carpels in the Pomegranate stand organically higher on the axis than the upper and larger carpels. One must not let the contradiction between the geometrical definitions of space and the organic relations lead us into error; but get a clear apprehension of this peculiarity. Only too readily are many authors to be noticed to whom this relation has never become clear; and thus, much else in the inflorescence and structure of blossoms remains to them obscure, and as a strange peculiarity, which a more correct apprehension renders very simple and natural. I shall have to enter more specially into this hereafter, when speaking of the blossom. This condition occurs, indeed, most strikingly in the internodes in the vicinity of the floral organs, but by no means exclusively, for it appears also earlier, as in *Melocactus*, *Echinocactus*, *Mammillaria*, &c., where the end of the axis exhibits an infundibuliform, or a cup-like form, and the terminal bud stands at the bottom of it, much lower than the ten or more preceding internodes.

II. In the second stage above distinguished, the equal expansion, in all directions, of the cells formed in the preceding stage, can alone act, since, still wholly imbued with moisture, the cells must be nourished tolerably equally on all sides. In this period, therefore, the volume may indeed alter, but not the form or relation.

III. In the third stage, lastly, the expansion of the existing cells is exclusively for the purpose of giving form. For the most part, indeed, expansion of the cells according to their kind is conditioned by the first formation in the first stage (§ 78.), since the cells become most intimately united in the directions in which they were in contact in the mother-cell; therefore, in other directions they are more loosely connected and afford less facility to the passage of sap, and consequently to nutrition. Certainly, so far as our yet imperfect observations reach, it is especially only the elongation of cells in the direction of the axis which essentially conditions and produces the form of the *developed* internodes; especially, therefore, do we find it connected with the conditions mentioned in *A* as existing in the first stage. If we measure the length of the cells in an internode (e. g., in *Arundo Donax*) which has just entered the third stage, and afterwards the length of the cells in a full-grown internode, we find at once that the expansion of the cells is quite sufficient to account for the elongation of the whole internode. Since, however, the cells enlarge unequally, we must only measure those in the middle; the result would be two small in the upper cells, and two great in the lower. The former expand less, and cease sooner; the latter, on the contrary, elongate more powerfully, and continue for a longer time to enlarge in the direction of their length: hence the so unfounded notion of many, that the internodes grow for a longer time at the lower end than at the upper.

All that is brought forward and enlarged upon in these paragraphs relates, of course, principally to the formation of the axis of the simple plants (of the second order), in which all the conditions described can actually occur in nature; it has also its application to those simple plants which originate as buds upon another, whether these become detached and continue to grow, or, remaining, form a compound plant with that on which they have been produced. Here again it is seen, that, as in the

simple plant, every single internode is capable of development independently into a special form; still more, the axes of the simple plants, in their combination into a compound plant, are independent of one another, and may assume wholly distinct forms, the combinations of which again are then specifically definite for plants and groups of plants.

In all this exposition, moreover, I would and could give nothing further than a general indication as to the course which nature here appears to take. Manifold as the researches on this point I have made are, and I believe they have been sufficient, provisionally, to justify what I have here published, yet must far more comprehensive and fundamental investigations be entered upon on this subject before the study of it can be brought at all to a conclusion. At present I know not of a single at all profound history of the course of development, even of any one stem; and hence it may readily be imagined how insufficient that must be which I alone have been able to work out in reference to this point. I have, however, indicated the necessary course of the investigation, and correctly exposed the question; the future alone can solve it, by the co-operation of many skilful powers.

*History and Criticism.* — As, in the foregoing, has been mentioned and too often indicated, the whole study of the stem suffers from the same errors as the other parts of Botany. The word stem has only an abstract meaning to most botanists, and thus is altogether useless in a scientific point of view. Here, as everywhere else, there is a want of accurate definition of ideas, because guiding rules for, and scientific regulation of, the process of definition are absent. Without a history of the course of development, and a definition of the conceptions obtained from this, we remain in this case, as in every other, without any fixed point, and cannot get beyond empty talking. One of the old school, for instance, says the stem (*stirps*) is divided into stock (*caudex*), trunk (*truncus*), stalk (*caulis*), Rush-halm (*calamus*), culm or haulm (*culmus*), scape (*scapus*), &c. When we divide in science, two things must be observed: first, that we divide according to *one* principle; secondly, that this principle be selected with reference to a purpose. The latter is to be determined inductively; the former is a purely logical inquiry, and its neglect a wholly inexcusable logical blunder. In this point, those common subdivisions are in the highest degree bad; they have no regulating principle whatever, and are quite as senseless and unscientific as the subdivision of vegetables in general into grasses, trees, roses, yellow flowers, green stalks, and plants. I should like to see, for instance, how the stalk (*caulis*) is to be distinguished from the culm (*culmus*) of grasses without anatomy, or, on the contrary, what anatomical characters one could find to distinguish the *scapus* of *Hemerocallis* from the *caulis* of *Lilium candidum.* It is quite a ridiculous misconception to treat of the *scapus* under the head of stems, since the sole character we can find for it is that of bearing flowers, consequently it is properly a flower-stalk or an inflorescence: under these circumstances, then, it belongs to the inflorescence and not to the stem; *spadix* would be just as much a form of stem as *scapus*, *calathium*, &c.

With regard to the second point, I have already expressed and brought forward proofs of my views, that in Botany we must unreservedly maintain the morphological principle as the highest. Therefore, we must derive the subdivision from this in the first place, and once more the course of development may alone be our guide.*

* Thus do we properly obtain the summary: — Phanerogamia. *A*, Monocotyledons.

The mode of speaking in question is altogether without scientific ground in another aspect. *Calamus, culmus, scapus,* &c., are quite isolated phenomena, occurring in certain plants, isolated groups, sometimes not in the whole of the group, and therefore they do not belong to general Botany, but merely to quite special parts of it. The Grasses have special forms of stem just like most other families, and it is merely a proof of logical confusion when a part of these forms are treated as something general in general Botany, which, if (as, however, has never happened) they are not designated as Monocotyledonous stems, have no marks of distinction from many other forms, nor even as Monocotyledonous, if, for instance, we place together the stem of *Mays* and *Tradescantia.* General Botany has nothing to do with all these peculiarities, and to treat them here, instead of directing attention to the fundamental laws of the development of form, is but a certain means of wholly confusing the learner, and giving him a barren host of words under the name of science.

Hence arise the many wholly fruitless contests, with which time and paper are wasted, as to whether a thing is *calamus, scapus,* &c. I am inclined to look upon those who would wish to distinguish them as if they said: *calamus* is the *scapus* on the *Cyperaceæ,* &c. Every discussion, without strictly scientifically defined conceptions, remains ever a useless bandying of words, necessarily devoid of results. Just one example may be brought forward here. Link * says: "The main stock (*caudex*) consists of parts growing *upwards,* which are called trunk and stem; and of parts growing downwards, the roots. The main trunk is that developing from the embryo; those which are developed from the buds are exactly like this, are called branches, and also grow upwards. Flowering stalks are branches. † The trunk grows upwards after it has taken root, since originally the germ grows downward ‡, sends out roots §, then it directs its other extremity upwards and grows in that direction, having grown downward previously." ‖ Next come definitions of the ramification of the trunk. "The direction of the ascending trunk is at first vertical, but it not unfrequently takes another direction afterwards." Different directions of the trunk and branches: "The length of the true ⸸ trunk is

*Structure,* closed (or definite) vascular bundles. *Axes: a,* with undeveloped internodes, 1, 2, and the rest of the varieties; *b,* with developed internodes, 1, 2, &c. varieties. *B,* Dicotyledons. *Structure,* unlimited vascular bundles. *Axes: a,* with undeveloped internodes, 1, 2, &c. varieties; *b,* with developed internodes, 1, 2, &c. For the sake of convenience, I have here united Monocotyledons and Dicotyledons in the consideration of single organs; and thus arises, but only apparently, the inconsequence that the division of the axes, according to closed or unlimited vascular bundles, appears to be more general and distinct than the morphological; but, as I say, it is only apparent, since the closed and unlimited vascular bundles give no principle of distinction at all for axial structures, but a distinction in the structure of the entire groups of plants. I mention this expressly here to avoid the accusation of inconsequence.

* Elem. Phil. Bot. ed. 2. vol. i. pp. 53. 221, et seq.

† What, then, is the branch of the Weeping Ash? what the horizontal rhizoma? what are runners? what the flowering stalks of *Arachis hypogæa,* &c.? *None* of which grow *upward.*

‡ Untrue: only the root, not the germ.

§ Untrue: most embryos have already a distinct root, which merely elongates.

‖ Untrue; since what grew downward (the root) never grows upward, and what grows upward has never grown downward.

⸸ Apparently only inserted to substantiate the meaningless statement which succeeds, since there is nothing about a division into true and false stems in the whole book. Besides, it directly contradicts what goes before; since the primary trunk of the em-

at the same time its height, since the long prostrate trunk of *Calamus Rotang* is a runner. * The tall Palms have a *cauloma.* † The stem of the Grasses originates in a different manner from that of the other Monocotyledons. The germ (*keim*, this is the name Link gives the cotyledon) is wholly wanting, or a scutellum ‡ appears in its place, which, *without bud* (!!), passes directly into the stem, which sends out roots below and grows upward above. § I should wish to retain the name 'halm' solely in reference to the following. The thick stem of *Mays* is very peculiar, proceeding, as out of a bud, from the apex of a stem exactly like the former, between the leaves. I would wish to call the upper stem halm ‖, did this not differ so much from the customary language, therefore I rather give this name to the former. This stem has a two-fold analogy with the stem and with the germ (*cotyledon*) of the other Monocotyledons." ⸸ Later on (page 301.) follow the so-called anamorphoses of the trunk. ¶ "The cauloma (palm-stem) occurs only in the Monocotyledons, and originates from leaves, which emerge one out of the other, and, in fact, from their sheaths. ** Merely a slender (!!) filament of stem unites these leaves ††. The number of leaves increases unceasingly, and thus the cauloma ‡‡ acquires increased thickness. But then that slender stem grows larger, since new parenchyma is formed, and in this new ligneous bundles. §§ Thus the cauloma does not become thickened upward ‖‖, but retains exactly the same diameter; nay, the lower portion is not unfrequently thinner than the upper, on account of the withering leaf-sheathes. ⸸⸸ The cauloma grows slowly, and plants which have it remain

bryo is certainly a true stem, and yet may be prostrate: in the twining stem the length and height are different.

* Whence does Link know this? To me it is very probable that this is the primary axis.

† Is not that a stem? No one has taken it for anything else yet.

‡ This scutellum is identical, in every respect, with the cotyledon in its development, and is never wanting in the Grasses.

§ Has Link ever beheld one single embryo of a grass and its bud which is distinctly separated from the scutellum?

‖ Why, is not evident.

⸸ If the germination of the oat be compared with that of maize, no distinction at all can be observed. The cotyledon (scutellum) does not become elongated: the large bud comes forth, in both, from the slit in the cotyledon; originally forms a developed internode; next some undeveloped, and then developed internodes; in short, there does not exist the slightest distinction when one examines accurately. If the germination of *Allium* and *Avena* be compared, one cotyledon will be found in both, and in both this encloses a formed bud, below a little slit. In *Allium* the cells of the cotyledon become elongated, so that the root, stem, and bud are removed somewhat from the seed; in *Avena* not: this is the sole distinction. But people must look into things.

¶ An expression equally superfluous and misapplied; for conditions of structure and differences of form are thrown together under it without distinction.

** Either false, or meaning nothing. The leaves never come out of leaves, but out of the stem. But in the Grasses, also, and in all plants with sheathing leaves, one leaf *surrounds* another.

†† Has Link ever seen a single Palm germinate, or examined a section through the active terminal bud of a *Yucca* or a Palm?

‡‡ The trunk of Palms and of *Yucca* never increase in thickness when once a sufficient base has been formed, but ascend vertically upward: the leaves originate on the thick, homogeneous, undivided mass of the rudimentary portion of stem in the terminal bud.

§§ This is diametrically opposed to the truth. Neither parenchyma nor vascular bundles ever grow, in unbranched Palm-stems, after they have passed out of the condition of bud.

‖‖ A direct contradiction of the statement a few lines before.

⸸⸸ This has no meaning whatever. If the cauloma, as such, is thicker above than below, it must have increased in size upward; if, however, it means that the cylin-

a long while devoid of stem; sometimes they never acquire one.* The Duckweeds have a very short cauloma, which grows out into a stem." † Next comes a third anamorphosis, the corm! The bulb is to be reckoned with this. ‡ Fourth anamorphosis, the rhizome. "From the base of the trunk, under ground, stems often come out which grow downward *from the first*," &c. §

What are all these anamorphoses? Are they stems, or not? If they originate from stems, what forms of stem precede them? What is the common character of the stem and its anamorphoses? what is its universal distinctive mark? To all the questions which immediately crowd into every even half-logical head, not one answer is to be found. But I think I have given enough of this. Superficial treatment of imperfectly observed facts characterises the whole of this exposition. Moreover, there are very many botanical manuals in which all is still more illogical and unscientific than here, and this may suffice for a general criticism of the whole existing literature of the stem.

No one has hitherto sought to elucidate the structure of the axis from its course of development; but, instead of this, space has been given to the strangest fancies, and it has even been asserted that the stem is nothing but a number of petioles grown together. One may, indeed, calmly declare that the people who assert such a thing do not understand themselves; since, otherwise, they would see that when they assert a blending together, they must point out, that is, demonstrate, how two separate parts become united by the process of growth, while they have not yet made one single search for such, the only possible demonstration. The investigation would clearly at once refute the affair. A portion of these men might readily come to their senses if they were only to trace one complete course of development. There is another portion, however, whom this will not render capable of clear vision. These are the people who think that they are able to make the forms with their words, instead of receiving them from nature. They do not suspect that natural history definitions, as a rule, are not artificially pieced together, but discovered inductively; and they feel themselves very clever when they can assert that the stem, which has always been an undivided whole, can still be regarded as compounded of petioles, although such is not the case. To this class Gaudichaud ‖ appears to belong, whose so-

drical cauloma is thicker with the leaves on than without them, it is a superfluous triviality.

* Above it is said, "The stem is never wanting." Here, however, is meant merely that they never acquire a long stem, which is also the case in other plants without a cauloma.

† I am unable even to form an idea of what similarity Link finds between a Palm-stem and a Duckweed. The latter never has any stem formed. The whole plant consists of one single internode, and there is no terminal bud to this.

‡ If Link had only observed with some attention the development of the stem of *Allium angulosum* or *senescens* from germination forward, he would have seen that there is not the slightest difference between it and the so-called cauloma of *Yucca*, leaving out of view variation of mass. In Palms and the species of *Allium* the lowest internodes die gradually; in the Palms only for a period; in the bulbs uninterruptedly, otherwise every bulb would become a Palm-stem. Link has recently, also, brought forward all this again as original wisdom in an otherwise worthless essay, without recollecting his former absurdities, and the correct views of others which already existed.

§ Above it is said all stems and all branches, at least at first, grow upward; nay, therein lay the solitary character of the stem.

‖ Gaudichaud, Recherches sur l'Organographie, la Physiologie, et l'Organogénie des Végétaux. Paris, 1841. Beyond all description, superficial and frivolous. (See my review in the new Jena Lit. Zeit. 1842.)

called new theory amounts to the harmless joke, that in future we are not to call the plant a plant, but a leaf; the leaf not leaf, but foliar-part leaf; the stem not stem, but stem-part leaf; and so on. I think we ought not to interfere with anybody's pleasures; but this is not science. Finally, we have a third class of naturalists, with whom there is no contending, who appear to have chosen their motto from St. Augustine: "*Credo quia absurdum est.*" These look down with a shrug upon the poor empiric who sees no more in things than his senses, his logical intellect, and his healthy reason show him. They argue thus: Just because the impression shows us the stem first and the leaf afterwards, it must be directly the opposite in the spiritual perception, which is directly opposed to the dim-eyed and rude perception of sense. These are the people who have bestowed upon us the nonsense of ideal abortions, and ideal blendings of parts, &c. There is no contending with them, because they recognise no conformity to law in our intellectual powers, consequently no deciding rules and no forum.

### b. *Varieties of Direction.*

§ 127. In germination, every axis of the simple plant (of the second order) developes straight upward from the ground on which it grows, so that a line which connects the extremities at the terminal bud and the radicle, describes a straight, or almost straight, line perpendicular to the plane of the soil, consequently, in most cases, to the surface of the horizon. The plants which germinate floating in water only apparently deviate from this law, because no fixed point is afforded them, in the fluid medium, on which they can erect themselves; therefore they develope horizontally (floating) even from the beginning. But this vertical direction only remains law for the further development of the axis when the latter has acquired, in proportion to its mass, a broad enough base, depending upon the mode of development of the lowest internodes, a secure attachment in the soil, depending on the requisite development of true or adventitious roots, and, lastly, a sufficient rigidity depending on the conditions of structure. The extreme and incessantly developing apex alone retains, throughout, the tendency to grow upward. Here, also, the conditions often alternate in the length of one and the same axis, according to specific peculiarities. For instance, the straight commencement is followed by some weaker internodes, then again by stronger which rise upward (*caulis adscendens*), or several stiff internodes are succeeded at the end by some lax ones (*caulis nutans*). In rare cases the originally vertical but weak internode is followed by firm tough ones, which grow forth always flat upon the ground, as, for instance, in *Nymphæa*, the axis of which never rises from the soil. Moreover, the axis in the course of its formation either grows out straight, or has a peculiar tendency to twine, whereby it appears to be twisted round its own axis when it grows free; or if in contact with a slender firm object, it twines spirally round this, and obeys specific laws as a left or right rolled spiral. Lastly

must be noticed that relation between two succeeding internodes where they do not lie in a straight line, but form with one another an angle which is often definite (*caulis geniculatus*). Very often the main axis, from being made up of undeveloped internodes alone, which gradually die from below upward, remains always under ground as an underground stem or trunk (*caulis, truncus hypogæus*).

It is wholly false to ascribe universally to nascent plants, a direction absolutely vertical to the earth. As the germination of *Viscum* on the side or under surface of a branch proves, the direction of the plant in general stands in no relation at all to the direction of gravity of the earth. The axis of every plant originally grows in a straight line away from the level of the soil in which it is fixed, and properly never alters this direction; but the internodes already formed often take another position, from the causes mentioned in the paragraph above. More remains to be said about this hereafter, under the head of Germination.

The causes of the spiral twisting of the axis round itself, or round a foreign object, as well as of the knee-like bending of the nodes, are altogether unknown. We have from Mohl * an excellent treatise on the point; but he was not able to discover the cause. I will here very briefly discuss the terms right and left wound stem, in regard to which much confusion prevails. The natural conception is this: The plant is developed from below upward, consequently it ascends; if, now, we use the expressions left and right concerning the plant, this can only have a meaning when we place ourselves in its position; but we turn to the left in ascending if we have the axis of revolution to the left, to the right if we have it to the right. If we refer it to the course of the sun, we can evidently, in regard to our northern hemisphere, only bring the southern half of each revolution turned toward the sun into relation with its course, and then the right wound spiral would go with the sun, the left wound against it. Linnæus † strangely used these terms in the opposite way, evidently starting from an obscure conception; and many others have followed him therein. Many have quite reversed the thing, called left right, and right left, till the whole matter had become confused. The reference to the course of the sun is moreover a very imperfect mark. It appears to me, however, that left and right wound cannot well be understood in any other way than that which I have given.

In conclusion I will add, that all the peculiarities here mentioned are equally shared by the axes originating from buds. In reference to the first point, it must be recollected that the bud is a plant, the base of which is limited from the very origin; that consequently the primary and natural direction of its growth is in a line perpendicular to the plane passing through its base. Sometimes, but not often, this direction becomes changed in the subsequent internodes into one parallel with the main axis.

### c. *Of the secondary Axis.*

§ 128. Buds may originate in the axil of every leaf (axillary buds), or, under favourable circumstances, at any point on a woody

* Von den Ranken und dem Winden der Schlingpflanzen.

† Philosophia Botanica, ed. 2. Gleditsch, p. 39.

trunk (adventitious buds); from these, as from the embryo, proceed perfect plants with axis and leaves, but, by reason of their origin, without radicle extremity; therefore, if they become independent, they become possessed exclusively of adventitious roots. Connected with the main axis these are called secondary axes; when annual, twigs or shoots; when perennial, branches; and the kind of combination in general, the ramification of the plant.* There are very few perfectly simple plants (of the second order); most are compound, at least in this way, that their buds produce flowers; but as every inflorescence arrests the further development of the axis, we may call those plants simple the axillary buds of which are *exclusively* flowers. The mode of ramification is the chief characteristic of the peculiar physiognomy of the whole plant (the habit, *habitus*). There is no regularity in the adventitious buds; but the position of the axillary buds is conditioned by the position of the leaves, and follows at once from this when all the buds are uniformly developed. But this does not often take place, since regularly appointed buds either remain wholly undeveloped, or form only transitory flowers, and thus are the same as undeveloped buds, at least to perennial plants. Thus in *Lemna* no terminal bud is formed, but only two lateral buds; these usually soon divide from the parent plant, and become developed in the same manner, and so on. *Viscum album* forms a flower-bud in every terminal bud; and as the leaves, and therefore the buds, stand in pairs upon the axis, the stem appears to be repeatedly bifurcated. In very many, especially of the perennial, Monocotyledons, it is regular for no axillary buds, except those growing into inflorescence, to come to perfection; thus, in most Palm-stems, and the so-called arborescent *Liliaceæ*, *Yucca*, *Aletris*, &c. The same occurs in some Dicotyledons, e. g., *Carica*, *Theophrasta*. Further, the varying rapidity and force of development determines peculiar forms. If the main axis is developed little or not at all, in proportion to the secondary axes, the so-called *caulis deliquescens*, the vanishing stem, is formed (as in *Prunus spinosa*); if all the secondary axes are developed with proportionately equal force with the main axis, the plant exhibits commonly a very long, ovate shape (*axis ramosus*), as in the Lombardy Poplar; if the lower branches are developed more quickly than the upper, so that all the points lie in one plane, the fastigiate plant (*axis fastigiatus*) results, and so forth. But the especially important point, as characteristic of the landscape, is the death of all the lower branches in perennial plants, whereby is effected the so characteristic separation of the tree into trunk and crown, or simple and ramified axis.

Finally, I have to mention here that the main axis very often dies soon after it has become developed out of the embryonal con-

* Inflorescence and fructification are really quite the same, namely, ramifications; inasmuch as the terminal shoots or twigs bear flowers, &c.

dition, while one or more of the lowest lateral buds grow on, and horizontally beneath or above, the surface of the soil, without ever erecting themselves, the axes proceeding from their lateral buds alone rising up free into the air. These horizontal axes proceeding from lateral buds, I name, exclusively, root-stocks or rhizomes (*rhizoma*). Examples are found in *Pteris aquilina, Equisetum arvense, Phragmites communis, Carex arenaria, Gratiola officinalis* (?), *Dentaria bulbifera* (?), &c.

The buds have to be treated at length hereafter; here merely the formation of axes was in question. On the relation of lateral parts (here the secondary axes) to an axis (here the main axis), what is requisite has already been stated and remarked in the General Morphology, as the forms arising out of it denote nothing exclusively botanical. Here it was merely necessary to mention what laws of development the varieties may depend upon. Very important it was, accurately to define the conception of a true rhizome, since, heretofore, the word has been so played with, that pretty nearly every possible part of a plant that ever is subterraneous has been understood by it, and at last no one knows what a rhizome really is, although the word is in general use. I think it is convenient to define and restrict the expression as in the paragraph. By this we shall have a name for a definite peculiarity in the mode in which many plants survive for a number of years, which certainly deserves a special name. The development of the rhizome is easiest to trace in germinating *Asparagus*. The systematists will object that they cannot begin with such distinctions in their dried plants. I cannot help them. The living plant is the object of our science, not the hay which we preserve as a miserable make-shift in our blotting paper; and a living, scientific principle, like the history of the course of development, can alone give Botany a value. Many, indeed, there may be to whom Botany is nothing but the science of the Herbarium: with these I have no concern.

### d. *Of the Structure of Axes.*

§ 129. Like all other parts of a plant, every axis, in its earliest condition, is composed of cellular tissue; in this are gradually formed the vascular bundles, closed or unlimited (see § 26.). This is common to all *Phanerogamia*. I know of no Phanerogamous plant (except *Wolffia* Hork.*) without vascular bundles (even if without vessels. § 26.).

Besides these, are formed, in different arrangements in different plants (§ 27.), liber-cells, sometimes as bundles, sometimes as a closed ring, or scattered singly in the parenchyma, intermediate forms between liber and parenchyma (§ 27.), sometimes isolated, sometimes in bundles; milk-vessels (§ 27.), and reservoirs for peculiar secretions (§ 24.), spiral-fibrous and porous cells (§ 18.), in groups or scattered; lastly, air canals and cavities (§ 24.), the former frequently regularly arranged, especially in aquatic and bog plants, the latter mostly occupying the axis of the internodes, as

* *Wolffia Michelii* mihi = *Lemna arrhiza* Micheli. *W. Delilei* mihi = *Lemna hyalina* Delile.

in the Grasses, *Umbelliferæ*, &c. Every axis is originally clothed with epidermis or epiblema (§ 29.), according to the medium in which it vegetates. On this, therefore, are frequently formed all the appendages of epidermoid tissue, especially glands, hairs, &c. and corky matter (§ 29.). The varieties resulting from these are so manifold, that, at present, it is only with great difficulty, if at all, that they can be treated generally; the varieties which result from the different arrangement and nature of the vascular bundles, are of more importance, and may be subjected to a more general examination. All vascular bundles are usually separated from their fellows by parenchyma; more rarely they form a perfectly closed circle. The separate bundles are either placed in a single circle (as in most Dicotyledons), or scattered in the parenchyma. The latter, again, collectively form a circle, which, like the preceding, encloses a definite portion of cellular tissue (pith) in the centre (e. g. in most Grasses, many *Umbelliferæ*, *Nyctagineæ*, *Chenopodiaceæ*, *Amarantaceæ*), or such an arrangement does not manifest itself (in cane-like Palms, Grasses with solid stems). The latter distinction seems to me very unimportant, since it varies in closely related plants, in one and the same family, e. g. in *Mays* (vascular bundles scattered throughout the parenchyma) and *Phalaris* (scattered vascular bundles enclosing a pith). In all cases where the arrangement of vascular bundles indicates such a boundary between included and excluded parenchyma, the inner is called pith (*medulla*), the outer bark (*cortex*). The portions of cellular tissue between the vascular bundles, maintaining the connexion between the pith and bark, are termed great medullary rays. In the simplest plants merely a central vascular bundle occurs, or a perfectly closed ring of elongated (vascular bundle) cells, like that in the Mosses, which, however, again encloses parenchyma in the centre (e. g. in *Ceratophyllum*). In flat stems, as in *Spirodela*, *Ruscus*, they lie in one plane (in a line on the transverse section). Consequently they both have merely bark and no pith.

The bark is composed, in addition to epidermis, of cellular tissue, in which we can in general distinguish merely an uniform parenchyma, but sometimes, especially in perennial axes, two layers; 1. the *outer*, which consists of elongated cells, with thick but almost gelatinous and generally porous walls, the boundaries between which are often quite undistinguishable, and the intercellular spaces of which are filled with intercellular substance; and 2. the *inner* layer, which is generally formed of roundish, thin-walled, lax parenchyma. In the latter alone occur reservoirs for secretions, milk-vessels, special forms of cells with special contents; in the former, scarcely anything but cells, containing homogeneous, colourless or red juices, and sometimes crystals. The two layers occur most distinctly defined in the trunks of which the cuticle does not form cork until a late period (as in the *Cactaceæ*); in other trunks and stems they very often pass gradually into each other. In front of the vascular bundles, in the inner layer of the bark, fre-

quently lie either liber-bundles, or liber-bundles carrying milk-sap, actual milk-vessels, or milk-sap passages. Since these often respectively exclude each other, while often there is no trace of any of them, the liber certainly cannot be called an essential constituent of bark (as the innermost layer); still more inaccurate would it be to term the cambium-layer, which much rather appertains to the vascular bundles, the innermost layer of the bark.

In trunks (Stämmen) the epidermis sooner or later forms corky substance, which is either gradually cast off in layers, as at first in the Birch, often merely becomes destroyed gradually by atmospheric influences, and thus, in part, acquires considerable thickness, as in the Oak, or, as often happens, the outer part of the inner layer of the bark and the outermost liber layer are thrown off together, and never reproduced. In the last case, new liber and internal cortical layers are formed annually, but with a peculiar form of cells resembling corky tissue; and the outermost are in like manner annually thrown off, as, for instance, in the Vine.

The pith, lastly, is composed of parenchyma alone, which, in its older condition, becomes thick-walled and porous. It often contains, also, solitary ramified liber-cells (*Rhizophora Mangle*), milk-vessels, reservoirs for peculiar secretions, &c.

The vascular bundles originate after the cellular tissue, in the same order as the latter; or rather, as the cellular tissue is gradually formed, a part of it passes gradually into vascular tissue. The direction of the vascular bundles wholly depends, therefore, upon the direction of the organising force. On account of this, also, the distinction between developed and undeveloped internodes, explained in § 126., forms the chief basis for the course of the vascular bundles. In the former, when the process of formation proceeds from below upward, in horizontal discs, the vascular bundles are straight, tolerably parallel to the axis of the internode, e. g. in *Tradescantia, Tropæolum;* where, on the contrary, one hollow cone is set upon another, as it were, in the terminal bud, the vascular bundles at their first development hold a course from the base to the apex of the cone, therefore from the circumference of the internode to its centre, and afterwards, as new internodes are superposed, the vascular bundles of the first cone are developed forward through the succeeding ones, to the circumference, where they enter the leaves or buds They make, therefore, a curve convex toward the interior, the length and convexity depending on the form of the terminal bud. The curve is very convex in *Yucca, Mammillaria,* &c.; more elongated in the Palms, *Dracæna, Iris,* &c. Since all new portions in the axis are formed outside the primary vascular bundles, whether they be increase of thickness to the vascular bundles, as in Dicotyledons, or the rudiments of new bundles, in Monocotyledons, the older and deeper vascular bundles, running towards the periphery to the leaves and buds, must necessarily cross the more superficial, ascending bundles, or their developing masses, which have originated outside them. This condition is naturally

most distinct when the vascular bundles are closed; but we see plainly enough, in *Mammillaria* or *Melocactus*, the bundles going to the basis of the lowest leaves, coming out from the most internal parts of the wood, and running past in a curve across all the subsequently developed parts.

At the point where a leaf is given off, in the Dicotyledons always, in Monocotyledons at most indistinctly, often not at all, several neighbouring vascular bundles become applied together, to form a loop (*ansa*), from the circumference of which pass off the vascular bundles of the leaf and the axillary buds.

Wood is formed from the unlimited vascular bundles of Dicotyledons, by their longer duration. The new cells originating between them, which correspond to the medullary rays, become again parenchymatous or medullary-ray cells, for these latter becoming compressed at the sides, by the enlargement of the vascular bundles, deviate somewhat in form from the common parenchymatous cells.

Frequently, however, one or more cells remain as parenchymatous cells, and so begin to form medullary rays in the midst of the wood (called *small medullary rays*), which sometimes go on developing for a long time, and sometimes cease at an early period. The wood does not generally grow uniformly continuously; in those parts, especially where, owing to climatal conditions, an alternation occurs every year between the active and dormant periods of vegetation, more vessels are formed at the beginning of the period of vegetation, and at its close wood-cells which are narrower and have stronger and thicker walls. By this means a division of the wood into more or less concentric hollow cylinders is occasioned, or those circles on the transverse section which are commonly termed *annular rings*.

In the Dicotyledons, where the vascular bundles are situated in several circles, they gradually unite together as they are successively developed, and form a close mass of wood, in which run then the separate vertical cords of the separate vascular bundles belonging to the cambium, giving the wood a peculiar appearance, which is beautifully exhibited in the species of the *Pisonia*.

There is but little that can be said generally of the composition of the axis from the separate forms of the elementary parts and of the tissue; all forms occur in the stem, and it is only in the case of individual groups of plants that we meet with certain forms or combinations specially or exclusively. Thus the *Labiatæ* are distinguished by having a square stem, the margins of which are formed by four strips of distinctly characterised cortical substance. The majority of the *Euphorbiaceæ* have milk-vessels, as the *Asclepiadaceæ* and *Apocynaceæ* are provided with their peculiar intermediate form between milk-vessels and liber-cells. *Nepenthes* is distinguished by having elongated spiral cells, which occur scattered in large numbers over every part of the stem. The distinction between pith and bark is not an universal essential characteristic for plants, as may be seen by the innumerable transition stages occurring between them. The two continually merge into one another.

That we only speak of medullary rays in the case of Dicotyledons arises from mere want of exactness of language, since the cellular tissue between the vascular bundles of the Monocotyledons is just as much a medullary ray as between the vascular bundles of the Dicotyledons, and as little changed in its cellular formation as in those Dicotyledons where the vascular bundles are very far removed from one another. Moreover, the cells in highly compressed vascular bundles, especially in the external parts of the stem of the Monocotyledons having a cambium circle, assume precisely the same form and arrangement as the medullary cells ranged in radial horizontal rows in the Dicotyledons, as, for instance, in the stem of *Aletris fragrans.*

We are able to assert very little generally concerning the structure of the bark, since nothing is unconditionally true, with the exception of the foundation being always composed of cellular tissue. No combination of definite forms of the elementary organs is peculiar to all barks; some forms occur, however, so frequently, that it would appear desirable to draw attention to them. Here I must, however, distinguish between Monocotyledons and Dicotyledons.

*A. Monocotyledons.* I am unable, from deficiency of a sufficient number of investigations, to say anything important of the structural relations of this group. As far as I know, the bark constantly consists exclusively of parenchyma, which is more elongated in the interior than towards the exterior — having more chlorophyll towards the exterior, but gradually losing it towards the interior, so that the cortical parenchyma constantly merges into the pith, wherever there is no sharp line drawn by the formation of a wholly closed circle of strongly thickened parenchymatous cells, which connects a ring of vascular bundles, as, for instance, in *Pothos.* According to Mohl*, most Palms have a peculiar layer, varying in thickness at different times, composed of thick-walled parenchymatous cells, placed immediately under the epidermis. In Grasses and the *Cyperaceæ* we find immediately below the epidermis separate bundles of liber-cells. The cells of the epidermis above these generally continue to have thin walls; whilst in those parts where parenchyma lies below, their walls become extremely thick, as, for instance, in *Papyrus antiquorum.*

*B. Dicotyledons.* 1. Annual Bark. In this we may, besides the epidermis, distinguish three parts of the bark; they do not, however, constitute anything essentially characteristic of the bark, which frequently only consists of a parenchyma, which at most merges gradually into a tissue similar to the external cortical layer towards the exterior. The three portions are the external and internal cortical layer, and the liber-layer.

Of the latter there is frequently not the smallest trace present, as, for instance, in *Cheiranthus Cheiri*, in a few species of *Solanum*, and most of the *Ribes*, in *Hedera* (?), *Viburnum Lantana, Mesembryanthemum*, in most of the *Crassulaceæ, Chenopodiaceæ*, &c. Where this liber-layer is present, it consists of isolated liber-cells (as, for instance, in *Cornus alba*), or liber-bundles (as in most Dicotyledonous trees), both being distributed in the cortical parenchyma, and generally in such a manner that their course corresponds accurately to that of the vascular bundles, or else it is composed of a more or less accurately closed circle of liber-cells (as, for instance, in *Syringa, Fraxinus*). Together with the liber-cells we

* De Palmarum Structura, § 12.

occasionally find milk vessels or passages, as, for instance, in *Rhus*. More frequently, liber-cells containing milk (in *Apocynaceæ*), or true milk vessels (as in *Ficus Carica*), or milk passages (as in *Mammillaria quadrispina*), take the place of the simple liber-cells.

The middle cortical layer, which is properly only traversed by the liber-cells and the parts by which they are represented, consists mostly of roundish, very loose cellular tissue, generally containing much chlorophyll. Here and there we find it ranged in vertical rows. Individual cells, or rows of cells, with crystalline accumulations, coloured juices, oils, &c., or with disproportionately thickened walls, are frequently interspersed: occasionally three or more cells, the uppermost and lowermost of which, being acutely pointed, form peculiar fusiform groups, and then usually contain peculiar substances (as, for instance, *Pinus sylvestris*).

The external cortical layer has hitherto, as far as I know, been entirely overlooked*; it appears, nevertheless, seldom to be wholly absent, and in a large number of plants, and groups of plants, it is so distinctly characterised, that it quite forces itself upon one's notice. It is only in a few plants that it has met with any attention, and there it has been described as a liber-bundle, although it really differs very materially from liber. The following are the characteristic marks of this tissue, as distinctive from cortical parenchyma. The cells of this layer are always vertical, elongated, very thick walled, but soft, and so far similar to liber-cells; they are, however, always applied *upon* one another by *horizontal* walls, seldom exceeding $\frac{1}{200}$th of an inch in length. They almost invariably exhibit more or less large pores, which frequently form distinct, beautifully ramified canals in the thick walls; they contain little or no chlorophyll, but merely homogeneous, colourless, or sometimes reddish juices, and here and there crystals. The cells are always connected together by intercellular substance, and their limits therefore frequently obliterated, so as to make them appear like apertures in a soft pulpy mass; when the cells are separated from each other, the intercellular substance shows itself with remarkable distinctness between them, as a secretion from them (§ 59.). This layer is found in many plants most strikingly developed, and sharply defined from cortical parenchyma, although in various modes of distribution: — 1. As a perperfectly closed layer (penetrated in some cases only by small canals opening into stomata), as in most of the *Cacti*†, *Melianthus major*, *Euphorbia splendens*, *Syringa vulgaris*, *Begonia argyrostigma*, *Ailanthus glandulosa*, *Rosa*, *Aristolochia Sipho*, *Piper rugosum*, *Cacalia ficoides*, *Cotyledon coccinea*. 2. Divided into many bundles, so that the green cortical parenchyma reaches the epidermis between them (in which case we find stomata there), as in the *Chenopodeacæ*, *Amaranthaceæ*, *Malvaceæ*, *Solanaceæ*, *Umbelliferæ*‡, *Justicia*, *Eranthemum*, &c. 3. Where it may be quite distinctly recognised as a special layer, but still passing quite into parenchyma at the borders, as in *Carya*, *Pyrus Malus*, *Pavia*, *Hedera*, *Acer*, *Daphne*, *Ptelea*, *Rhus*, *Viburnum*, *Cornus*, *Ficus*, *Sempervivum globiferum* et *laxum*, *Sedum pallidum*, *Cotyledon arborescens*. 4. More completely merging into cortical parenchyma, and therefore less

* Hartig maintains that he was the first to draw attention to this tissue; as, however, the researches on which he grounds this claim are at present unknown to me, I am unable to say with what justice. However, I attach less to being the first to observe a thing, than to observing it correctly.

† See my papers on the Physiology and Anatomy of the *Cacti*.

‡ The so-called liber-bundles are beneath the epidermis in these five families.

distinct, as in *Ribes, Alnus, Elæagnus, Juglans, Populus, Salix, Carpinus, Castanea, Corylus, Quercus, Cytisus, Cornus mascula, Sambucus, Rhamnus, Tilia.* 5. Finally, I have found this layer either entirely absent, or only to be recognised in the external cellular layer, as in *Cheiranthus, Hippophäe, Mesembryanthemum,* and the so-called tree-carnations. On the whole, the external cortical layer seems to stand in a definite relation to the formation of cork, and to be more sharply defined in proportion to the tardiness with which the latter appears (as, for instance, in *Cactaceæ, Aristolochia Sipho, Cacalia ficoides*): the contrary, however, also occurs, as, for instance, in *Mesembryanthemum.*

2. Perennial Bark. The development of the vascular bundles from the cambium is always accompanied by a similar development of the bark, since a part of the cells that have newly originated in the cambium attach themselves, towards the interior, to the vascular bundle, a second part continues to develop as cambium, and the remainder attaches itself externally to the old bark. Thus we find that, similarly to the annual rings of the wood, definite layers of bark are formed in every period of vegetation, being composed, according to the peculiar character of the primary bark, of mere parenchyma, liber and parenchyma, or of alternate layers of parenchyma and liber, or of alternating layers of true parenchyma and such as is interrupted by liber-bundles. From this the layer of liber frequently becomes broader towards its inner side, in proportion as the wood thickens, so that the liber-bundles exhibit a beautiful wedge-like appearance in a cross-section. This new formation of bark is, however, marked by great specific differences: in some plants it is rapid and decided, as, for instance, in the Lime-tree; in others very slow and partial, as in the Beech. The thickness of the bark depends partly upon this, and partly upon the following causes: sometimes, even in the first period of vegetation, and then generally uniformly, the epidermis is developed into a cork-tissue (as in most trees); less frequently this occurs later, in that case beginning at separate spots, and extending itself by degrees, as, for instance, in the *Cacti* and leafless *Euphorbiaceæ* (§ 29.). The cork-tissue varies in hardness and durability. It most frequently consists of tabular cells, already described in the First Book, which are sometimes thickened in alternate layers, as, for instance, in the *Cacti;* and more rarely somewhat radially elongated, as in the Cork Oak, or Cork Elm. In the last named, and in the Maple, it acquires considerable thickness, but at the same time is easily destroyed by atmospheric influences in the case of the Maple. In its usual form it generally lasts longer, and becomes frequently very thick, constituting the so-called bark of the tree, as, for instance, in *Quercus Robur.* Occasionally the cork is found in the bark, in the condition of separate layers of an easily destroyed tissue, in which case it falls off in horizontal bands, or shreds, having a specifically definite form.

In some stems new layers of a parenchyma, very similar to cork-tissue, are developed from the cambium (?) with cortical parenchyma (in *Ribes*), or alternately with cortical parenchyma and liber (as in the Vine): this parenchyma (termed *periderma* by H. Mohl) likewise contains easily destroyed layers, so that the whole external bark drops off, and then, as in the case of cork-formation, layers of periderma and liber are successively shed. (This is strikingly exemplified in *Pinus sylvestris.*) We are, however, very deficient in the necessary investigations. We have to thank H. Mohl for the first exact work on this point.* I have

* On the Origin of Cork and Bark. Tübingen, 1835.

myself endeavoured to throw additional light upon the origin of the cork-layer.* The first formation of the periderma is still, however, very obscure.

The pith consists essentially, and very generally, of parenchyma, without any manifestation of special layers in it. When old it becomes either very thick-walled and porous, or it is destroyed, and then leaves large air-cavities, as, for instance, in many Grasses, *Umbelliferæ*, &c. There frequently remain alternate, isolated, firmer layers of pith, and thus form an air-cavity divided off into chambers placed horizontally one upon the other, as, for instance, in *Juglans regia*. Interspersed in the pith we find spiral cells, thick-walled porous cells, cells with peculiar juices, milk-vessels, air-passages, and even, in the case of *Rhizophora Mangle*, peculiarly-branched liber-cells. † In many of the woody *Rosaceæ* there are peculiar vertical and horizontal rows of very thick porous cells, &c., in the pith. Innumerable plants yet remain to be investigated. Many more isolated phenomena might be noticed, but nothing can be made of them at present. ‡ Vascular bundles alone, with one exception, are found in *every axis*, and, consequently, these are almost the only parts of which the distribution and nature are susceptible of general treatment. In the first place, we must mention one common difference affecting the nature of the vascular bundles, and their relative mass compared with the cellular tissue of the axis. The vascular bundles either preponderate in mass, and their elementary parts are generally very much thickened, and the axis, having thus greater firmness, is termed a woody stem or stalk; or the vascular bundles are present only in a proportionately small mass, separated from each other by larger quantities of cellular tissue, and their component elementary parts, in a great degree, or principally, have thinner walls, and then the whole mass of the axis is softer, the thinner lax or still flexible, and the stem or stalk is termed succulent: the last-mentioned is also, with superfluous diffuseness, called *herbaceous*. In the succulent axes the course of the vascular bundles is generally much more simple and regular, as may be seen in the different internodes of the one and the same axis (which may be woody below and succulent above). The distinction between a woody and a succulent axis agrees still less with that of stem and stalk. We often find in the same class some species having succulent, and others woody stalks; and not unfrequently a whole family have exclusively succulent stems.

The arrangement and course of the vascular bundles are, however, the most important points to be considered. In the main paragraphs I have given the general features, but I will here enter somewhat more specially into the question, as, at the same time, I separate the individual groups. I add the following particulars as the general result of *my own* researches on this subject, without, however, maintaining that they are to be received as the ultimate expressions of a natural law: —

1. The origin of any vascular bundle, as well as the development of one already extant, presupposes, without exception, the presence of a cambium-layer, as every new formation of structure, in and upon the plant, presupposes the existence of a process of cell-formation. By cambium, cambium-layers, formative layers, we understand nothing more than a cellular tissue, which has not yet ceased to develope new cells, in contra-

* On the *Cacti*, loc. cit.

† Wiegmann's Archiv. Jahrg. v. (1839), part i. p. 232.

‡ As, for instance, the remarkable gelatinous (?) masses, beset with crystals, lying in special cells, found in the epidermis of *Justicia*, and in the bark and pith in *Eranthemum*.

distinction to those tissues in which there is no longer normally any process of cell-formation going on. The latter consist in such cases either of living parenchymatous cells, in which, under favourable influences, such a process of cell-formation may recur, as, for instance, in the germination on Monocotyledonous leaves, &c., or of relatively dead, very woody cells, in which such a process of development can never be revived, as, for instance, in the older part of a vascular bundle, wood, &c.

2. In all cases we find that the new cells in the cambium-layer, and the new vascular bundles, or the thickening mass of the older vascular bundles, are developed from the base towards the apex of the axis, from the older into the new internode, and from the main to the secondary axes, but never the reverse.

3. Only in the *Gymnospermæ*, Monocotyledons, and Dicotyledons does a cambium-layer occur in the circumference of the axis; and where this is present it forms the limits between bark and pith or medullary cellular tissue. In the Monocotyledons this cambium-layer only occurs as an exception, and is, of course, independent of the separate, invariably definite, vascular bundles; in the *Gymnospermæ* and Dicotyledons this layer is never wanting, and is so constituted that the cambium of each separate vascular bundle of the simple or outermost ring also belongs to the general cambium-layer, and is connected by the cambium masses, in front of the medullary rays, into one continuous layer. Moreover, every individual, unconnected, isolated vascular bundle, has its own cambium.

4. The main difference must still be deduced from the nature of the vascular bundle, which corresponds with the great natural divisions of plants. Other distinctions that have been advanced are untenable, and are based upon deficient observation of all existing conditions.

5. All asexual *Gymnosporæ* can grow upward only, owing to the deficiency of a cambium-layer. All *Gymnospermæ* and Dicotyledons grow in thickness as well as height. In the Monocotyledons we find both conditions, sometimes manifested exclusively as terminal growth, and then, again, the latter combined with continuous increase in thickness. From this we cannot, however, deduce any classification of the Monocotyledons, since both conditions are met with in the same family, as, for instance, in the *Liliaceæ* and in branched Palms (?).

## I. *Asexual Gymnosporæ.*

These all agree in having simultaneous vascular bundles, and, as far as I know, in that no cambium-layer occurs in any stem, by which the latter might be further thickened when once formed. The structure is in general very simple. Liverworts and Mosses have only a simple central vascular bundle, without so-called vessels. The *Lycopodiaceæ* have only a central vascular bundle, generally forming an irregularly-lobed figure in the transverse section, this being occasioned by the arrangement of the vessels. The vascular bundles, going into the leaves, run for a time upward in the bark before they enter the leaf. The stem of *Isoëtes* is formed in a very different manner, and here we find a *ring* of vascular bundles, undeveloped internodes, and a constant and successive dying off from below. Mohl has made very exact observations on this subject.

Ferns have an extremely deficient stem-formation, exhibiting sometimes developed, and sometimes undeveloped, internodes; in all, however, there is but a simple ring of vascular bundles. The vascular bundles rise vertically in the developed internodes, and, at the starting point of the

vessels of the leaves, form loops by their mutual combination, from which these are given off. In the undeveloped internodes they rise up in serpentine lines, forming, by their alternate approach and retreat, longer or shorter, narrower or broader, meshes, from the edges of which the vascular bundles of the leaves branch off. These latter not unfrequently run for a time upwards in the pith, before they pass through the meshes and enter into the leaves. H. Mohl has given us minute anatomical observations on the Fern-stems, but we are unfortunately still wholly deficient in a history of their development.

The *Equisetaceæ* have all developed internodes and a simple ring of vascular bundles. We are still without any very exact observations, or special history, of their development.

## II. *Sexual Plants.*

### A. Rhizocarpeæ.

These, again, have an extremely simple structure of stalk and stem, together with a central vascular bundle, which contains only a few weakly-developed vessels.

### B. Gymnospermæ.

The whole of this division is devoid of stalks, having only stems. The *Cycadaceæ* have only undeveloped, and the *Coniferæ* and *Loranthaceæ* only developed, internodes. All have a cambium-layer under the bark on the outer side of the simple vascular bundle ring, and the stems are consequently capable of being indefinitely thickened; the vascular bundles are indefinite. In the *Coniferæ* we find a ring of vascular bundles (the medullary sheath of older botanists) surrounding a pith, which even in the first year close into a woody cylinder (fig. 157. *h*, *k*). The portions of wood corresponding to the vascular bundles run quite perpendicularly, and only leave very narrow crevices for the escape of the little bundles, branching from the inner part of the vascular bundles, which intersect the wood obliquely, and ascend for a time into the bark before they pass into the leaves (fig. 157. *h*, *i*). These points will be made more plain by means of the accompanying diagram of a section of a piece of the stem of the Fir. The *Loranthaceæ* do not appear to differ in their arrangement from the *Coniferæ*.

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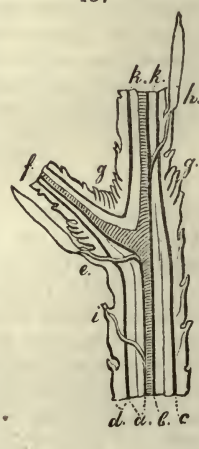


In *Cycas revoluta* we find also a simple ring of vascular bundles, from the innermost part of which the vascular bundles for the lateral parts run through long meshes (which are formed by the alternate retreat and closing together of the vascular bundles,

157 *Abies excelsa.* A longitudinal section of the apex of a tree, of two years' growth in the lower part, and only one year's growth above the lateral branch. *a*, The wood divided into two annual portions (annual rings). *b*, The medullary sheath; that is to say, the oldest portion of the first annual ring, or original vascular bundles. Between *a* and *b*, the pith, shaded with cross lines. *c*, Cambium-layer. *d*, Bark. *f*, Lateral branch. *e*, A leaf, from the axil of which the lateral branch has originated. *g g*, Re-

rising in undulating lines), into the bark, describing an arc somewhat convex upward and towards the interior; these vascular bundles do not, however, pass directly into the leaves, or leaf-scales, but first compose, parallel with the periphery, arcs of vascular bundles, running *horizontally:* from these, distinct vascular bundles branch off for the leaves. The very unimportant materials at my disposal did not allow of my extending my observations further.

## C. Monocotyledons.

The most simple plants of this division have no vascular bundles, as, for instance, *Wolffia:* those nearest allied amongst the *Lemnaceæ* first exhibit definite indications of these; in *Spirodela* we even find them combined with spiral vessels, but distributed in a plain surface as the necessary accompaniment of a flat stalk. Many of the *Najadeæ*, as, for instance, *Najas*, *Zanichellia*, *Ruppia*, have only a central vascular bundle. In the remainder we meet with the following modifications: —

### 1. Developed Internodes.

The stalks and stems have always several rings of vascular bundles (fig. 158. *d*), which occasionally enclose a pith, where a circle of vascular bundles are connected by a ring of thickened parenchyma. This is often the most external (usually) (fig. 158. *c*), often a more internal one, as in *Pothos*. A portion of the vascular bundle passes through the nodes into

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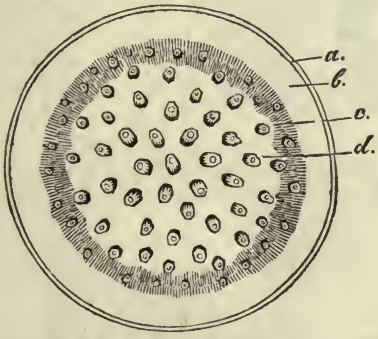


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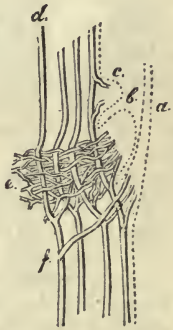


the leaf, whilst a part rises into the next internode (fig. 159. *d*). Small twigs branch off from all the vascular bundles that pass through the nodes,

mains of the scales of the bud: the one to the right only for the terminal bud of the preceding year; to the left for this, and also for the axillary bud, from which the branch has arisen. *h*, A leaf at the one year old portion of the stem, together with the adhering vascular bundle. *i*, Base of the leaf on the second year's portion of the stem, with the vascular bundle appertaining to it. *k k*, Wood of one year's growth.

158 *Ruscus aculeatus.* Transverse section of the stalk. *a*, The epidermis. *b*, The bark. *c*, A ring of thickened cells, by which the external vascular bundles are connected into a continuous zone, and thus separate the pith and bark. *d*, Vascular bundles scattered through the pith.

159 *Zea Mays*, natural size. A section made lengthwise through a macerated portion of the stalk. *a*, The leaf. *b*, The axillary bud. *c*, Adventitious root. *d*, Vascular bundles, in their course from below upward: they give one branch to the leaf, and another, or several, to the nodal plexus (*e*), and to the bud (*b*).

forming a confused plexus in the node, which, for the most part, merges into the axillary bud (fig. 159. *e*). The innermost vascular bundles in the nodes supply the lowest leaves, the external bundles the upper ones, as in Grasses, the cane-stemmed Palms, and the *Commelinaceæ*. There are many groups that have not yet been examined. The whole of the vascular bundles in the same internode are simultaneously formed and developed, and the internode itself, when perennial, does not continue to increase in thickness, whether the plant becomes branched or not. The primary, like the secondary, axes only grow upwards; in fact, they are devoid of a cambium-layer.

## 2. Undeveloped Internodes.

The stalks (in *Pistia obovata*, for instance), and the stems of Palms, herbaceous *Liliaceæ*, bulbs of *Allium*, *Lilium*, &c., have a conical terminal bud, sometimes longer, and sometimes shorter, in accordance with which the vascular bundles run from below and the exterior, upward and towards the interior, and then from thence upwards and externally, to pass into a leaf (fig. 160. *d* and *e*). The arc, which is convex towards the interior, is longer or shorter according to the length of the terminal bud; and the vascular bundle likewise passes through a longer or shorter portion of the whole axis, according to the same conditions.

In the full-grown stems of the Palms, the vascular bundles connected with the upper leaves do not reach the base of the stem, notwithstanding the length of the arc. In the simplest case the vascular bundles are wholly isolated; they are, however, more frequently connected by intermediate branches, seldom from within externally, but often laterally with

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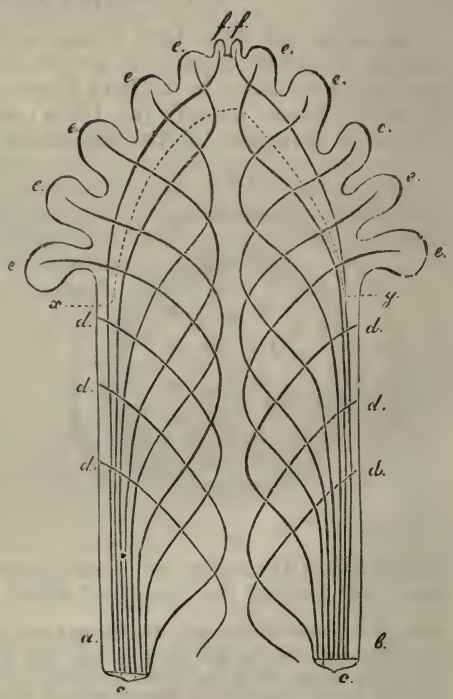


[160] Diagram of the course of the vascular bundles in the monocotolydenous stem, with undeveloped internodes, and roundish, conical, terminal bud. *a—b*, The lower, fully developed, part of the stem. *c c*, External firmer portion of the stem formed by the closer course of the vascular bundle. *d d d*, Vascular bundles running as far as the cicatrices of leaves that have died off. *e e e e e*, Leaves in the bud in the order in which they are developed, with the vascular bundles belonging to them. *f f*, The latest-formed leaves: all that is cut off by the line *x—y* above the stem has originated at the same time with the pair of leaves (*x x*).

one another. From this cause, as well as from a more or less extended vertical course of the vascular bundles before they form the arc, the external part of the stem is composed of a thicker cylinder of vascular bundles (fig. 160. *c c*), whilst the inner portion, composed only of arcs, becoming more and more isolated toward the centre, and cellular tissue increasing in quantity in the inverse proportion, appears much looser. However simple we may consider the course of the vascular bundles in the Monocotyledons in judging of them according to H. Mohl's researches *, it is, in fact, but seldom so; nevertheless, H. Mohl's representation affords the simplest and clearest delineation, and gives the type from which all the analogous structures must be deduced. Occasionally, however, the course actually appears as direct as that indicated by the diagram, as, for instance, in the subterranean stem of *Iris chinensis* (fig. 161.). The separate vascular bundles, especially so far as they form the arc, by no means always run in one and the same vertical plane, their emergence deviating frequently about 50° and

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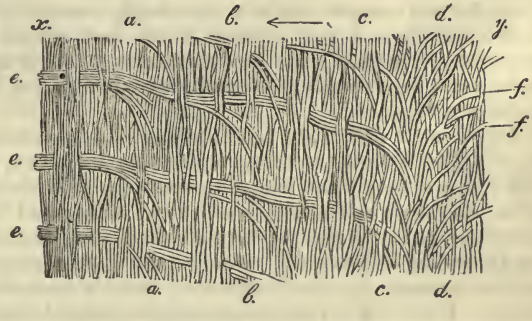


more, of the circumference of the stem, laterally, from the vertical of their starting point, as may be easily observed, for instance, in *Yucca gloriosa*. The *Xanthorhœa australis* (fig. 162.) appears to me to differ most strikingly from the simple type of the stem. Here the fascicles of the vascular bundles, emerging into the leaves (*e, e, e*), evidently have a threefold origin from three different zones of the stem (*aa, bb, cc*). Quite in the interior another plexus of vascular bundles

* De Palmarum structura.

[161] *Iris chinensis*, natural size. Longitudinal section of the subterranean stem. *a a*, Cortical layer. *b b' b''*, Three leaf cicatrices. *b''' b'''' b*v, Remains of three leaves which have been cut off, with the vascular bundles running to all six leaves. *c*, Youngest leaf, still in the bud stage: to the right may be seen the terminal bud as a scarcely perceptible elevation, at the right side of which the next leaf will be formed.

[162] *Xanthorhœa australis*, natural size. Longitudinal section through half the diameter of a piece of stem (*x—y*). The arrow indicates the direction from within outwards. The course of the separate vascular bundles has been carefully exposed by artificial preparation. *a, b, c*, The three regions of the external part of the stem, which give off vascular bundles for the cords (*e e e*) running into the leaves. *d*, The inner lax part of the stem, with very irregularly inclined vascular bundles, whose course

appears, the course of which, however, I could not make out, as the piece in my possession was not sufficiently large for me to trace it. Still it appeared to me that the vascular bundles, *f, f*, had not yet quite reached the middle of the stem. It will at least suffice to draw the attention of more favoured observers to this striking structure, and will give a better representation of it than the miserable trash of Gaudichaud (Plate X. figs. 10. to 15.). Perhaps the history of the development of *Aletris fragrans* will afford the first some conclusions on the point: — An old stem of about 4·25 Paris inches in diameter consists of two parts: the primary stem, about 7 lines in diameter, in which the vascular bundles exhibit the usual arc-like course; and an external, much more solid zone, gradually formed by the cambium-layer. The vascular bundles passing from within to the leaf-cicatrices permeate this external layer in a perfectly horizontal direction. The external layer becomes divided, however, again into four zones, which produce the appearance of annual rings when seen in the transverse section. The three external ones are, when taken together, of about the same thickness as the fourth internal one: they differ in this, that in the external ones the fibres do not ascend vertically but obliquely, consequently in a spiral round the axis, and wind towards the left; in the second in like manner, but winding towards the right; in the third, again, turned towards the left, and finally becoming gradually horizontal in the fourth. I may remark here, that whilst the parenchyma is arranged in vertical rows in the primary stem, it appears to be in horizontal rows between the external vascular bundles, in the manner of the medullary rays.

An essential difference presents itself here, according as the formative layer is limited to the terminal bud (above the line *x*, *y*, in the woodcut fig. 160.), or whether there is a continuous layer in the whole circumference of the stem below the rind, which is then bounded internally by it. The latter occurs in the case of normally-branching stems, as, for instance, in the *Dracænæ*, *Aloineæ*, and *Aroideæ*, the former in normally-simple stems, as, for instance, in the *Tulipaceæ*, and Palms with undeveloped internodes. Beautiful investigations on this subject may be found, accompanied by the carefully selected results of earlier observations, in Unger (see his Bau und Wachsthum des Dikotyledonenstammes, Petersburg, 1840, page 34.).

I must finally make mention of the singular stem-formation in the tropical *Orchidaceæ*. A large portion of these, such, for instance, as are commonly described as having tubers, have not very thick stems (generally branched), with abbreviated internodes. Those branches, however, which come to blossom, produce a peculiar form that has hitherto been known as tuber (knolle). Either *one* of the more central internodes of the blossom-bearing branch swells into a disproportionate mass of very varying shape, or all the lower internodes of the branch form a longer or shorter, more or less thick, fleshy mass. In both, as, for instance, in *Epidendrum cochleatum* and *Bletia Tankervilliæ*, the regular course of the vascular bundles may be distinctly observed, but in the case of the last-named plant (I know not whether the same holds good for all similarly formed) there is a peculiar vascular system intended for the new lateral buds. Little branches pass from the external vascular bundles,

appears most enigmatical in the case of those which, like *f f*, have not yet reached the middle of the stem, when they cease, as in the drawing.

and run together in a horizontal direction below the rind, from both sides up to the buds. On cutting vertically through one of these stems, we find a transversely severed, strikingly large group of vascular bundles below the rind, corresponding to each internode. It unfortunately happens with the *Orchidaceæ*, as with the *Cacti*, that it is a matter of difficulty to obtain a sufficient quantity of material to ascertain the anatomy or its history of development.

## D. Dicotyledons.

### I. *Stalks.*

The stalks frequently exhibit no essential differences from those appertaining to Monocotyledonous plants, since the distinction of the unlimited or indefinite vascular bundles is often imperceptible in the growth of one year. But the vascular bundles generally close in the first year into a simple circle, and the external parts in several circles to form a ring, so that the parenchymatous masses separating the individual bundles are compressed together into medullary rays. In most cases the vascular bundles run from below upward in straight parallel lines. They form a loop where the leaf begins, the edges of which furnish vascular bundles for the leaf and the axillary bud, and the pith of the bud is thus brought in connection with that of the stem by means of their opening, as in the case of *Tropæolum*. The vascular bundles supplying the leaves and buds generally separate from this loop exactly at the point where they enter the leaf. Sometimes, however, they first pass through a longer portion of the parenchyma of the pith or the bark (as in the *Amaranthaceæ* and *Chenopodiacæ*).* In perfect nodes, loops of vascular bundles are seldom found passing across the stem; in general the parenchyma merely appears to be tougher and closer at these points. We are here, on the whole, very destitute of accurate investigations, more especially with regard to the first year's stalk with undeveloped internodes.

### II. *Stems.*

#### 1. Developed Internodes.

##### A. *With a simple Ring of vascular Bundles.*

Here the vascular bundles very seldom run parallel, but generally in serpentine lines, alternately approximating and retreating from each other; the meshes thus formed are filled by the medullary rays. Where liber-bundles lie in front of the vascular bundles they follow the same course.† Large and small medullary rays, and annual rings, are formed in the manner indicated. Wherever there is a leaf, one large or several

* Very admirable observations on this last-named point may be found in Unger, Bau, &c., des Dikotyledonenstammes, Petersburg, 1840.

† In this manner is formed that beautiful network which used formerly to serve the West Indian beauties as a natural lace veil, and which was derived from *Daphne Lagetta* (*Palo di Laghetto*, Lace bark tree, *Bois de dentelle*).

smaller loops are formed (fig. 163. *B*), from whose circumference the vascular bundles are given off for the leaf and axillary bud, while the openings furnish parenchyma for the formation of the bud. The vascular bundles of every newly developed internode stand in immediate connection with, and are immediate prolongations of, that portion of the vascular bundle of the preceding internode still capable of development, and thus the cambium of the vascular bundles forms a continuous net through the stem and branches of the whole plant. During the developments of the vascular bundles of the stem, and those connected with them, and belonging to an axillary bud that grows into a branch, the base of this branch becomes more and more covered with newly formed wood. We thus see the same condition established as in the Monocotyledons: an under lateral branch crosses all the layers of wood passing to the upper parts. The difference is merely, that in the Dicotyledons they are portions of the continuous mass of the progressively developing vascular bundles; while in the case of Monocotyledons they are discrete parts, new vascular bundles. The wood is very various in its composition (§ 26.).

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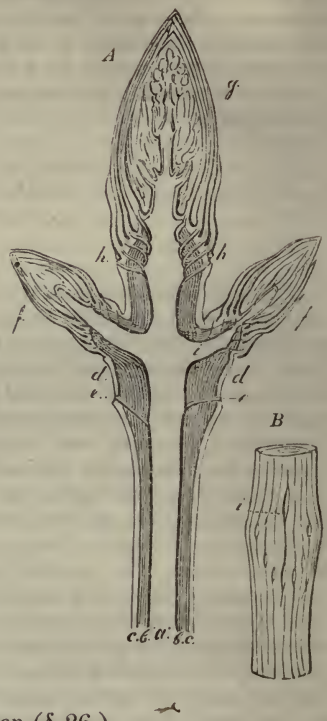


B. *With several concentric Rings of vascular Bundles.*

As far as I know, this condition is only met with in *Piper* (?) and *Pisonia;* and, perhaps, in a few of the *Crassulaceæ,* as in *Crassula.* The separate vascular bundles continue to grow, and finally close into a firm woody mass; each, however, retains its own cambium, and likewise a small portion of parenchyma, not perfectly dislodged: such, at any rate,

[163] *Æsculus Hippocastanum,* natural size. *A,* A longitudinal section of the end of a twig some time before the bursting of the bud: *a,* the pith; *b,* the wood; *c,* the bark; *d d,* cicatrices of the uppermost leaves of the former year; *e e,* the vascular bundles of these leaves; *f f,* the axillary buds of these leaves, with their scales, and the vascular bundles belonging to them; *g,* terminal bud of the twig, ending in a blossoming panicle; *h h,* cicatrices of the lowest scales of the bud which have fallen off, together with the axillary buds already visible: somewhat above this, the still-closed scales, together with their vascular bundles; *i,* medullary mass, which enters into the axillary bud. *B,* Deeper part of a twig in the region of a leaf cicatrix, and a (severed) axillary bud, the bark removed from it on the side turned towards the spectator: *i,* crevice between the portions of the wood for the passage of the medulla into the bud. Below this crevice there are seven others, lying in a semicircle, for the escape of the vascular bundles destined for the leaf.

is certainly the case in *Pisonia*. An old stem of *Crassula* (?) which I once examined seemed to bear some resemblance to this. Here the wood consisted entirely of wood-cells. Many separate vertical cords of parenchyma were seen scattered through this mass, each having from two to three spiral vessels.

All the conditions touched upon here still require a minute study of the history of their development.

### C. *Stems of Climbing Plants.*

The stems of many tropical climbers (*Lianes, Llanos*) exhibit a peculiar structure, which has long been misunderstood. Even in our own indigenous plants we meet with some indications of it. In the first year, most of them exhibit nothing striking, if we do not regard the generally square stalk as such; and we find that they have a simple ring of vascular bundles, which closes towards the end of the first period of vegetation into an ordinary wood cylinder. In the following years, however, the peculiarities are more and more strikingly manifested, consisting in the wood not being uniformly developed towards the exterior throughout its whole circumference, but ceasing to grow at definite parts, often regularly, and as frequently in a fantastically irregular manner, allowing the substance of the bark to replace it. In this manner stems are produced, which, in a transverse section, exhibit the most varied distribution of the wood. We meet with the first indications of this peculiarity in our indigenous species of *Clematis* forming stems (fig. 164.), in the strikingly broad and regularly arranged large medullary rays (*a*); and in the six narrower portions of wood (*b*), which are not nearly so fully developed towards the exterior as the six broader ones (*d*). To these we may add the *Bignoniaceæ*. After the wood has continued for some time to be regularly developed, it ceases growing in four different places (figs. 165—167. *a*), so that the bark is no longer pushed outward; and on the further development of the wood in the remaining places, the bark forms, in the transverse section, four septa of variable thickness between the four portions of wood.

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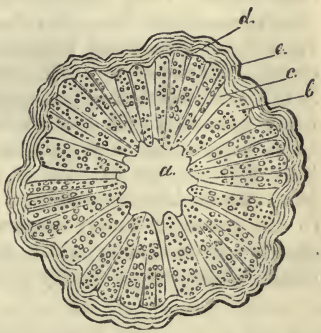


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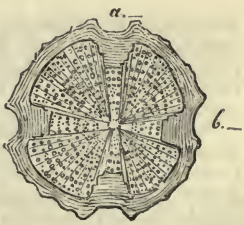


In some species these cortical masses become a definite degree broader in each succeeding

[161] *Clematis vitalba.* Transverse section of the stem. *a*, The pith. *b*, The smaller wood-bundles. *c*, The large medullary rays. *d*, The larger wood-bundles. *e*, The bark.

[165, 166, 167] Transverse sections of stems of the family of the *Bignoniaceæ*, natural size. At *a* we see the wedge-shaped cortical portions entering between the wood.

[165] The four interposing portions (*a*, *b*) may be plainly seen even by the naked eye.

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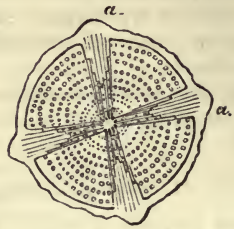


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annual ring, so that a sharply marked step is formed on each side (fig. 166.); in another species all that is formed are four very thin, flat plates, wholly separated (in consequence of drying) from the wood (fig. 167.). Gaudichaud* collected this stem, and has drawn it, like the rest, very rudely. Link† says, "In order to form a branch, a portion of the wood accompanying the pith turns to the side, and, by its increase, forms the branch. Sometimes the young branch goes out from a three or four year-old stem or branch, separates the layers, and thus makes its appearance on the surface. It is then seen as a wedge in the wood of the old branch, which is larger or smaller according to the modification of the branches. If the nodes stand in a cross [how can the nodes stand in a cross?] four wedges are seen standing opposed to each other. Very large wedges of this kind are found in the stems of the *Bignoniaceæ* from Rio Janeiro, such as I now have before me." If Link here means the portions of stem mentioned, coming from Gaudichaud, this is but an evidence of sad superficiality. Still more striking is the cross-section of many climbers of the family of *Sapindaceæ*. A hasty glance would lead us to imagine that we had here a cylinder of wood surrounded with bark in which other stems or branches with their bark had become blended in their growth (figs. 168, 169.). A minute observation, however, refutes this view at once from the absence of pith in the exterior woody masses. It is especially peculiar here, that, as appears from Gaudichaud's showy pictures, this separation of the wood is not continued uniformly throughout the whole length of the stem, but

* Loc. cit. tab. xviii. fig. 4. According to him, *Bignonia capreolata* would exhibit the same phenomenon; and this is to be found in some botanical gardens. A history of the development of this peculiarity is very desirable.

† Element. Phil. Bot. ed. 2. vol. i. p. 273.

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They consist of parenchyma, and concentrically arranged bundles of very much thickened gold-coloured liber-cells: the wood exhibits no annual rings. The medullary rays are present in the wood-wedges, which form, as it were, the continuation of the interposed portions of the bark; but they are far less conspicuous. The wood, besides the wood-cells, contain also some parenchymatous cellular tissue.

[166] The tissue of the wedges (*a*, *a*), passing in by step-like gradations from the bark, is very remarkable. It exhibits distinct medullary rays, which are continued from it to the pith, whilst they are very indistinct in the rest of the wood. Between the medullary rays there are bundles of thick-walled and densely porous parenchymatous cells (similar to many liber-cells; as, for instance, in *Cereus*), and a great number of very broad, thin-walled, scarcely perceptible, porous cells, whose steeply ascending transverse septa exhibit strikingly evident reticulated fibres, the interstices of which are filled with a membrane, closely beset with fine pores.

[167] The narrow intervening pieces of bark (*a a*) consist here of but little cellular tissue, and a greatly preponderating quantity of liber. Annual rings are not distinctly traceable in the wood. The wood consists principally of parenchyma, having only thin bundles of wood-cells.

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in places (at the nodes?) the woody masses merge partly into each other, while the separation occurs again in a different mode of distribution. Finally, the most astonishing phenomena are seen in the families of the *Aristolochiaceæ* (fig. 170.), *Asclepiadaceæ*, *Malpighiaceæ*, and the *Bauhiniæ* (fig. 171.), in which, in the transverse section, the woody mass appears divided in the strangest ways by cortical substance, separated into various portions, and often elegantly lobed. A great part of these aberrant forms of stem were brought home by Gaudichaud from his voyages, and he has represented most of them in a very negligent manner in his superficial book. A. de Jussieu has made better use of these materials, having inserted a most excellent investigation of the Lianes in his monograph of the *Malpighiaceæ*, in which he has, by ingenious use of the few materials for the history of development that were at his command, at least traced up these singularities to the general type of the Dicotyledons. I pass by here a few other abnormal conditions, as, for instance, the *Phytocrene*, described by Wallich (Pl. Asiaticæ rariores),

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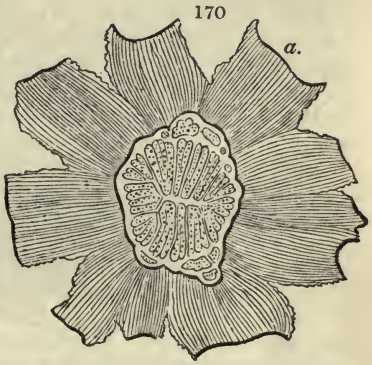


[168, 169]. Transverse sections of stems from the family of *Sapindaceæ*, natural size. *a, b,* Woody masses, wholly separated by bark from the main stem (*c*). In fig. 168. these are homogeneous throughout; but in fig. 160., on the contrary, arranged radially around a cellular tissue occupying the middle, intermediate in character between pith and medullary ray cells.

[168] The annual rings are wanting in the central portion, as in the three peripherical masses: the medullary rays are not very striking, and run in waving lines. The peripherical portions have points (in one lying excentrically) from which medullary rays pass out, but are without trace of pith.

[169] Here, also, the crescentic marks in the five peripherical wood-masses are the places whence medullary rays set out; but these places are not composed of cellular tissue: the linear arrangement of the wood-cells is continued through them, and even porous tubes occur in the middle of them. The lines, however, in which the wood-cells lie, make a slight curve at their entrance and exit from the crescentic mark; and thus this originates as a mere optical phenomenon.

[170] *Aristolochia biloba.* Transverse section of the stem. *a,* Considerably developed, deeply torn cork, magnified about four times.

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because, from want of material, I could say nothing of importance about them, and I look upon mere guessing as a most objectionable method in Botany.

The great diameter of the porous tubes may, apparently, be regarded as a general peculiarity in the ligneous structure of all climbing plants. These have also strikingly large pores which (as I have never yet seen in vessels) form even ramified canals, as is seen particularly well in *Bauhinia.*

## 2. Undeveloped Internodes.

These have scarcely been investigated at all in the Dicotyledons. Most of them remain very short, since they die below as they increase upward. They belong principally to the subterraneous stems and

[171] *Bauhiniæ spec.* Cross-section of a stem one-third of the natural size. *a*, Wood-masses, partly with strikingly large porous tubes. *b*, Cortical substance. *c*, Bundles of true wood, arranged in a simple circle, very evident on account of their whitish colour, with straight radial medullary rays. The principal masses form eight larger portions of wood, the cross-section of which resembles more or less a Japanese fan, with an almost always distinguishable pedicle of cortical parenchyma, and at the same time traversed in the interior by anastomosing streaks of cortical substance. With the exception of the circle of vascular bundles (*c*), the rest of the wood is chiefly composed of parenchyma; and the medullary rays run in curving lines. The cortical tissue contains liber-cells and liber-bundles, even to the very interior of the stem. The wood-bundles (*c*) do not run vertically, but obliquely laterally; yet the section in my possession is only about a line thick.

rhizomes. The leafless *Euphorbiaceæ*, *Carica*, *Theophrasta*, *Nymphæa*, and *Nuphar*, as well as many *Cactaceæ*, afford excellent material. I at present know of no other researches in reference to this point, except my own very imperfect ones into the stems of *Cactaceæ*, especially *Mammillaria*, *Echinocactus*, and *Melocactus*. The vascular bundles at first make an arc of considerable curvature; by the gradual development of the pith the curvature becomes almost effaced, and it only remains in the upper part, where the vascular bundles pass off to the leaves. The first succeeding layer developed in the vascular bundle is applied over and up beyond this, dividing at the point where the primary vascular bundle goes off to the base of the leaf, and uniting again above to pass up to the base of a leaf situated higher up. The next layer of structure forms in the same way, by splitting and reuniting, two meshes, one for the primary vascular bundle, and one for the portion of the first layer of increase running to the upper leaf, then above this it runs up to the base of another leaf. This structure is continued up throughout the whole stem, which thus possesses a form of wood exhibiting perfectly regular meshes or areolæ, which appear to be formed by an alternating superposition of vascular bundles, and each give passage to a bundle coming from the innermost part of the wood. Of course, there is here a perfect crossing of the vascular bundles going to the lower leaves by all the subsequently formed portions of vascular structure, and by a little care we may make preparations not very unlike the structure of a Monocotyledonous stem with undeveloped internodes. The whole structure bears great similarity to that of the arborescent Ferns, allowing for the different nature of the vascular bundles and the difference of dimension.

Many interesting varieties in the structure of the wood occur here also; and the wood of the *Mammillariæ* and *Melocacti*, composed entirely of peculiar spiral-fibrous cells, is particularly worthy of notice.

The stems of the *Rhizantheæ* (Blume) appear to be altogether aberrant and irregular in their structure; I cannot say anything about them, since I have no material, and I refer to the researches of Unger and Göppert presently to be named.

Even Moldenhauer * remarked, that one and the same vascular bundle varied in its structure in different parts of its course. As a general rule, we may say that in the Monocotyledons the vascular bundles are simplest in their lower part, often, for instance, in the Palms, composed at that part solely of elongated parenchyma (liber); in the middle becoming more complicated from within outward, exhibiting almost all the forms corresponding to the varied expansion of the cell; above, they become simpler again, particularly where they pass off into a leaf or branch, and consist frequently merely of such elements as correspond to a considerable expansion in the longitudinal direction after the appearance of layers of thickening. In the Dicotyledons the vascular bundles appear to have a tolerably uniform structure below and in the middle, but toward the upper end the onward developing portion of each older bundle passes into the form of a primary bundle, or, in other words, every primary vascular bundle of a new internode appears as the immediate prolongation, not of the primary bundle of the preceding internode (which rather runs to a leaf), but of the layer of increase of

* J. J. P. Moldenhauer, Beiträge, &c.

this, the elementary portions of which do not correspond to any expansion in the longitudinal direction.

*Literature, History, and Criticism.*

We possess few or even no general fundamental researches into the history of development of axial structure. Most authors present merely anatomical investigation of dead specimens. I refer here to the following as the only important essays that I know of: —

*J. J. P. Moldenhauer*, Beiträge zur Anatomie der Pflanzen. Kiel, 1812. An analysis of the stalk of Maize, masterly in every respect, considering its time.

*H. Mohl*, De Palmarum Structurâ. Monachi, 1831.

*H. Mohl*, Untersuchungen über den Mittelstock von *Tamus elephantipes* L. Tübingen, 1836.

*Unger*, Ueber den Bau und das Wachsthum des Dikotyledonen-Stammes. St. Petersburg, 1840.

*Unger*, Beiträge zur Kentniss der parasitischen Pflanzen. Ann. des Wiener Museum, vol. ii. 1841.

*Göppert*, Ueber den Bau der Balanophoren, &c. Act. Acad. L. C. N. C. vol. xviii. Suppl. 1841.

*Göppert*, De Coniferarum Structurâ Anatomica. Breslau, 1841. (See my review in the Neuen Jenaer Allg. Lit. Zeit. 1842, No. 15.

*Schleiden*, Beiträge zur Anatomie der Cacteen. From the Mém. de l'Acad. Imp. des Sc. de St. Pétersbourg p. div. Sav. vi. ser. t. iv. (Leipsic, Engelmann, 1842).

*Miquel*, Ueber den Bau der Melocacteen, Linnæa, Bd. 16. (1842), p. 465.

*Harting*, Bydrage tot de Anatomie der Cactëen (Tydschrifft voor naturlyke Geschiedeniss an Physiologie door van Hoeven en de Vriese, Bd. IX. 1842).

*A. de Jussieu*, Monographie des Malpighiacées. Paris, 1843. (Contains excellent investigations on the structure of stems in climbing plants.)

*Naudin*, On the Rhizome of *Narcissus Pseudonarcissus* in the Ann. des Sc. Nat. 1844. Ser. iii. t. i. Botanique, p. 162—176.

*V. Martius*, Ueber den Structur des Palmenstammes, Münchn. gel. Anz. 1845.

Many isolated notices, not connected or compared according to any leading principle, are to be found in Meyen (Physiologie), Bischoff (Botanik); and in Treviranus (Physiologie), especial abundance of the literature of the subject.

Almost all that has been said by isolated authors is wholly useless, either because they have had no regard to the history of development, or, if they have noticed this, have spoken so indiscriminately of growth, increase and enlargement, without distinguishing whether new cells have originated, cells already existing expanded, or merely become transformed into different tissues by the alteration of the form and configuration of their walls.

Two notions there are especially which have long sadly confused our science, from which a correct method would have completely saved us, since both were, at least at the time, and in the species on which they were built up, wholly unfounded fables, having no connection with any guiding principles, and consequently never should have assumed scientific

perspicuity, much less, as did happen, have served as a temporary basis for theories pervading the whole science of Botany.

The first is the idea of Desfontaines of the distinction between Monocotyledons and Dicotyledons, that the former develope new structure in the centre of the axis, and grow in the inside (*plantæ endogenæ*), while the latter produce ligneous substance close under the bark, and deposit it on the inner side, and thus grow on the outside (*pl. exogenæ*). All this had no greater foundation than the fact that in the Monocotyledonous axis the vascular bundles are farther apart in the centre; consequently, in the preponderance of parenchyma, the substance is more lax. It was not ever attempted to make even a superficial observation of the process of growth; if it had been merely observed that the vascular bundles going to the lower leaves, consequently the older, crossed those going to the upper leaves, which must be the younger, a child might have been made to understand at once that a growth of new vascular bundles in the interior was an absolute impossibility. Nevertheless, upon this empty fancy, which a child might have refuted, De Candolle built a grand system of vegetables, which it never did require the distinguished and comprehensive researches of Mohl to overthrow.

The second notion is that of Du Petit Thouars, which was not less ill-grounded, which, as expressed by him, would be upset by every, even the most superficial observation, and even in its more refined subsequent statement is by no means established, but has important and apparently irresistible objections against it. Du Petit Thouars thought that all increase of thickness of the axis resulted from the descent of roots from the buds. Such a crude notion scarcely required refutation. On the other hand, it was afterwards stated that the formless but organisable substance (the cambium) was gradually organised from the buds downwards. The only possible foundation for this view, namely, evidence obtained by thorough investigation of the history of development, is still due from all its assertors, the latest, Gaudichaud, &c., included. Therefore it is already to be set aside as devoid of foundation. But the contrary can be made good, that, in the first place, no cambium ever exists as a formless fluid in the plant, unless we would so call the cytoblastema enclosed *in the cells;* secondly, that, so far as observation at present reaches, cells are always formed in cells, that this cell-formation, according to the observations I have made in the *Cactaceæ*, &c., progresses from below upward; thirdly, that the axillary bud is already formed in the terminal bud before the axis begins to increase in thickness, and that certainly the cells of the bud are organised into vascular bundles from the vascular bundles of the stem upward into the bud, and not in the reverse direction. By these remarks the whole notion seems to me to be for the present set aside, and it would require quite other support than that which Gaudichaud's imperfect attempts in anatomy and physiology could give it.

Lastly, I must notice the most recent views of Martius on the structure of the stems of Palms, &c. Martius asserts, that here the vascular bundles, the primary structure of which is sketched out in the conical terminal bud, on the whole, as I have already explained it (Wiegmann's Archiv, 1839, 219.*), do not merely grow upwards into the leaves, but also downward, by their lower end, in the stem. These facts I must

* Beiträge zur Botanik, vol. i. p. 29.

entirely oppose from my own observations. Hitherto I have never had an opportunity of investigating living Palms, or more than small fragments of dead ones. But from what I saw I believe I may venture to conclude that the stem of Palms does not essentially deviate in such a way from those of other Monocotyledons, that one may not transfer to the Palms, in the main points, the laws of structure found there. Now, so far as I know, such a process of growth does not occur in *any* Monocotyledonous plant. According to my observations the newly produced vascular bundles merely grow continuously upward. In advancing the distinction of limited and unlimited bundles Martius follows me, but, in my opinion, he has not conceived nearly clearly enough the distinction between developed and undeveloped internodes, and in particular he has not formed a clear conception of the peculiarities of the stem with undeveloped internodes, and the conditions of structure resulting therefrom. Moreover, he has left the meaning of the term onward growth (Fortwachsen) of a vascular bundle equivocal. If it means that the already existing elongated cells become transformed into vascular bundles, it describes no peculiar process of growth,—the vascular bundles were already to be distinguished in their elementary condition; but if it means that the cells themselves, of which the vascular bundles are composed, are produced subsequently, originating above first and proceeding downward, this is, I believe, erroneous. It is necessary to bear in mind the essential distinction between Monocotyledonous axes with and without a cambium circle, in order to understand these structures. Where no cambium exists there are no other new cells formed besides those in the point of the bud. But where there is cambium, all development, and so also the development of new vascular bundles in the stem, proceeds upwards and outwards, never, so far as I have been able to observe, downwards or toward the interior. The lowest and innermost cells are always the oldest, never the upper or outer (of course excluding the bark, to which alone an endogenous growth can be ascribed). I must therefore distinctly assert, that in the Palms, as in all Monocotyledons, the lower end of an older vascular bundle never reaches down into an internode lower than that in which the lower end of its first rudiment originated.

### e. *Review of Axial Structures and Terminology.*

§ 130. The following distinctions appear to me to be of importance from the points of view treated in the foregoing paragraphs.

#### 1. *Duration.*

A. Annual. Stem (*caulis*).
Internodes (*internodia*).
- *a.* Only existing in the beginning of the period of vegetation, fugacious (*internodia fugacia*).
- *b.* Enduring the whole period (*int. annua*).
- *c.* Only existing in the latter part of the period of vegetation (*int. serotina*).

B. Perennial. Trunk (*truncus*).

2. *Position on the Soil.*

A. Above ground (*epigæus*).
B. Under ground (*hypogæus*).

3. *Form.*

A. Developed internodes (*int. elongata*).
B. Undeveloped internodes (*int. abbreviata*).
C. Disciform expanded internodes (*int. disciformia*).
D. Concavely expanded internodes (*int. concava*).

N. B. Rigid, pointed, leafless, or defoliated internodes are called spines (*spinæ*); soft, curling, and thus climbing round foreign objects, tendrils (*cirrhi, capreoli*).

4. *Various Internodes of the same Axis.*

A. Bearing true leaves and branches (*caulis* and *truncus*).

N. B. Sometimes no leaves are developed (*axis aphyllus*), or they fall off from the *truncus*, mostly at the end of the first year (*axis denudatus*). The stem may grow out from the terminal bud of an embryo, as in the simple stem, or out of a trunk. A stem produced from a trunk might be called *scapus;* but this is a wholly superfluous term.

B. Bearing only bracts, bracteoles, or flowers, peduncle (*pedunculi*); in a compound inflorescence the internode bearing a single flower is called the pedicel (*pedicellus*). *Receptaculum* is a superfluous expression in the *Synanthereæ, pedunculus disciformis, conicus*, &c., is simpler and more correct. Also in *Ficus, pedunculus concavus.*

C. Internodes between calyx and pistil, receptacle (*torus*), e. g., in some *Rosaceæ, torus disciformis* (in *Potentilla*), *torus concavus* (in *Rosa*).

*a.* Internodes between calyx and stamens (e. g., in *Rubus*), or calyx and corolla (e. g., in *Passiflora*), the disc (*discus*), e. g., *planus* (in *Geum*), *d. tubulosus* (in *Cereus grandiflorus*).

*b.* Internodes between corolla and stamens, androphore (*androphorum*), e. g., *a. elongatum* (in *Cleome*).

*c.* Internodes between stamens and pistil, gynophore (*gynophorum*), e. g., *g. conicum* (in *Rubus*).

D. Internodes between calyx and seed-buds, as a hollow disc enclosing the seed-buds, inferior germen (*germen inferum*), e. g., in *Synanthereæ, Orchidaceæ.*

E. Internodes between stamens and seed-buds, as a plate with the borders curved inward together, in the cavity of which the seed-buds occur, stalk-pistil (*pistillum cauligenum*). In *Liliaceæ* and *Leguminosæ* (?).

F. End of the stalk in the germen, as support of the seeds, spermophore (*spermophorum*), in seed-buds (*gemmulæ*). (For the parts of these see below, under the Seed-bud.)

### 5. *As to the Nodes.*

A. With imperfect nodes (*caulis, truncus*).
B. With perfect nodes.
  *a.* Stalk (*culmus*).
  *b.* Stem (*calamus*).

N. B. It is exceedingly useful to mark this distinction by definite terms: but then we must name the stalk of the *Caryophyllaceæ*, most *Umbelliferæ* and *Labiatæ, culmus;* the stem of *Bambusa, Calamus, Piper, Aristolochia,* &c., *calamus.* In other respects the expressions *culmus* and *calamus* have no sense, since it could only be defined as a stalk, such as occurs in the plants to which such a stalk is ascribed, the former, namely, in *some* Grasses, the latter in *some Cyperaceæ.**

### 6. *Different Axes of Compound Plants.*

A. Main axis produced from the terminal bud of the embryo (*caulis vel truncus primarius*).
B. Secondary axis, produced from axillary or adventitious buds (*c. vel tr. secundarius*).

N. B. Still connected with the main axis, called branch or twig (*ramus*).

C. Ramification of the axis (*ramificatio*). Ramification of the *pedunculus* (*inflorescentia*).
D. Secondary axis growing along underground, and *its* secondary axes alone rising above the soil, root-stock, rhizome (*rhizoma*).

N. B. For secondary axes which lie upon the earth, because they are too weak to stand erect, there are some special terms, but these appear to me superfluous: —*flagellum, stolo, sarmentum,* runner, sucker, which are sometimes to be distinguished by the foliation, sometimes by the rooting, now one way and now another, and again may be different from the *caulis repens, humifusus, prostratus, procumbens, decumbens, sarmentaceus,* and all the rest of this manufactory of words, and yet cannot be separated by any characters.

E. It is useful to discriminate, according to the ramification and duration,
  *a.* The simple plant, the lateral buds of which are flowers (*herbula*), e. g., *Cuscuta, Myosurus:*
  *b.* The branched stalk, herb (*herba*), e. g., *Anagallis, Veronica verna:*

* How thoughtlessly a part of the terminology was made and applied cannot be seen more strikingly than if we ascribe a *calamus* to most of the species of *Scirpus, Carex,* &c., which, if *scapus* had any meaning, would fall altogether within its definition.

*c.* With underground stems, stalks above ground, undershrub (*suffrutex*), e. g., *Aconitum Napellus, Pœonia officinalis:*

*d.* Stem branched from below, without predominance of the main stem, bush (*frutex*), e. g., *Prunus spinosa, Juniperus Sabina:*

*e.* Trunk, the lower branches of which soon die, and which only bears a crown, tree (*arbor*), e. g., *Pyrus torminalis, Fagus sylvatica.*

N. B. We also reckon among trees those stems also which branch from below upward, but in which the main axis is developed in far the greatest proportion, and may readily be traced to the summit, e. g., *Populus dilatata, Abies excelsa.* These might even be called *arbores fruticosæ.*

## C. Foliar Organs.

### a. *Foliar Organs in general.*

§ 131. The leaves (*folia*) also may be divided into annual (*folia annua*) and perennial (*f. perennia*); the former again into deciduous (*f. decidua*), which live only in the early part of the period of vegetation; yearling leaves (*f. annua sensu stricto*), which live through the whole period; and late leaves (*f. serotina*), which are not perfected till toward the close of the period. With few exceptions every plant has temporary leaves, namely, the cotyledons and frequently those next following them. The *Orchidaceæ*, some species of *Cuscuta**, and some *Cactaceæ*, are the only plants at present known with certainty to be destitute of cotyledons. Others, for instance the *Rhizantheæ*, have not yet been sufficiently investigated. Many plants are wholly destitute of foliar organs between the cotyledons and the peduncles of the flowers, as, for instance, all the *Cactaceæ*, excepting *Peireskia*, and some species of *Opuntia;* in others these are annual, as in *Alnus*, or perennial, as in *Pinus.* The floral parts, the leaves last perfected, exist in all Phanerogamous plants.

I. The general character of all foliar organs lies solely in the history of development, as already has been shown (§ 120.). It follows from what was said there, that the leaf is, as it were, pushed out from the axis; that the summit is its oldest, the base its youngest part. It follows, moreover, that the power of development in a leaf is limited, and never persists long when the terminal shoot becomes removed from it by onward growth. Finally, observation of the course of development also shows that the foliar organ is altogether determined by the axis, as a definite product of the fashioning organisation,—that a protracted duration of the process of development may indeed somewhat increase the volume

* In *Cuscuta monogyna*, for instance, the embryo has distinct foliar organs. *C. americana, arvensis, congesta, epilinum, epithymum, europæa, nitida, umbrosa*, have no trace of them.

and influence the internal structure, but never can change the destined form. Thus, consequently, the leaf is the form, determinate in its growth, and therefore morphologically, which proceeds from the fundamental element of the plant, the axis, indeterminate in its growth, and therefore morphologically indeterminate: this definition includes all foliar organs, and excludes all axes.

I do not think that it will be possible, in the first place, to find a more strict expression of the distinction between leaf and axis than is here given, yet I feel deeply that it is very far from being the only correct and sufficient one: but here again we require a much deeper penetration into the history of development than up to this time has or could have been attained (see Plate III., figs. 1—11.). Progress will first become possible when we have resolved the whole process of formation in the leaf into the history of the formation of its individual cells, which, as the most difficult task in all Botany, will yet remain long unperformed. At the same time it is not to be denied, that the distinction between leaf and axis is the sole scientific basis for the whole morphology of the *Phanerogamia.* It has certainly been more easy to comprehend this since Goethe's Metamorphosis of Plants has conjured up a presentiment of the morphological unity of the law of formation, but little has yet been done for the strict and scientific comprehension of the matter. As I have already observed, the cause of this is the want of philosophical, especially logical, exposition; for it is not noticed that the obscure ideals of the imagination must be elevated into conceptions capable of definition by inductive method, to fit them for a properly scientific treatment. How little our text-books fulfil this purpose has been already remarked. Let us take another example: Link * says, "'A leaf,' says Joachim Junge, 'is that which expands upward, or in length and breadth, from the place at which it occurs, and the boundaries of the third dimension of which, that is, the inner and outer surface of the leaf, are different from each other.' This definition excellently marks all foliar parts." That this pretended excellent definition does not at all apply to the parts of the flower (which certainly are foliar parts) is clear, but it does not apply to any leaves of Pines, of *Mesembryanthemum*, *Sedum*, *Opuntia*, nor to the scarious stipules of the *Paronychiaceæ*, &c. Link says, further: "The main distinctive character of leaves is the position beneath the buds. Every true branch originating from a bud," (yet only from an axillary bud,) "is supported at its base by a leaf. . . but all leaves do not support branches." How, then, does Link know that these are leaves, when they are deprived of their principal distinctive character? No science will be advanced in this way, but merely groundless chattering stereotyped.

II. When the leaf emerges from the axis it is a little conical body, the base of which gradually comes to occupy the entire circumference of the axis, a stem-embracing or amplexicaul leaf (*f. amplexicaule*); or it shares the circumference of the axis with one or more other leaves, which have originated with it on the axis in the same plane, whorled leaves (*f. verticillata*); or, lastly, it is confined to a small portion of the circumference, without any other leaves

* Elem. Phil. Bot. ed. 2. vol. 1. p. 410.

arising from the axis in the same plane, scattered leaves (*f. sparsa*). These three positions of the leaves upon the axis are, most undoubtedly, the primary ones occurring in the plant. We find the first in the cotyledon of the Monocotyledons; the second in the cotyledons of the Dicotyledons. But if we disregard, in the Monocotyledons, the character of embracing the stem, only looking to the fact that one leaf alone is formed at one level on the stem—if we trace the further development of the leaves of Monocotyledons, and of those of most Dicotyledons, since in the latter it is only in a few groups that the later leaves are formed in whorls,—we find that the great majority of plants have scattered leaves. If every vegetable axis be regarded as a cylinder, the bases of the leaves must admit of being connected by a spiral line. More minute investigation, then, shows that the distances of the bases of the leaves on this spiral are not without law; but a certain regularity may be observed, and, in fact, the angle (angle of divergence) made by two planes, passing through the middle of the axis and the bases of two adjacent leaves, which angle therefore is the measure of the distance of these leaves from each other, is on an average 137° 30′ 28″, consequently a number bearing no ratio to the circumference of the stem (360°); so that no two leaves ever can be exactly in the same vertical line. In the course of the entire axis the distances of the turns of the spiral alter, but always regularly, sometimes even on account of accidental influences; and thus from the simplest fundamental condition proceeds an infinite multiplicity of modes of manifestation, even when the various forms of the axis do not interfere. Compare but the rosette of leaves of *Sempervivum tectorum*, the stalk of *Lilium Martagon*, a shoot of *Populus dilatata*, a cone of *Abies excelsa*, and the fruit peduncle of *Helianthus annuus*, which latter exhibits the regular position of the leaves even through its fruit which originate from axillary buds.

The study of the position of leaves has recently occupied so many excellent labourers, that it indeed cannot be attributed to the want of talent or applied industry if the results obtained are at present so little satisfactory or certain. Rather have we to seek the cause in the inaccurate methods, and, secondly, in our as yet so imperfect knowledge of the nature of plants generally, especially of the laws of their morphological development. In reference to the first point, it must be remarked that observation and research have been restricted wholly to isolated, determinate conditions of the developed plant, when the abortion of particular parts has so frequently already destroyed the regularity of the rudiment, while at the same time the recognition of this fact has opened the door to fancy, so that when the phenomena would not exactly suit themselves to a preconceived hypothesis, this has been supported by a supposed abortion of the parts. Two very opposite paths have been struck out, one by the Germans, Schimper and Braun, the other by the French, the brothers Bravais. Schimper and Braun examined a countless multitude of cases, sought by the most accurate measurements possible to obtain a series of results, which they used as a basis for an

induction, and believed that they thus discovered that, in an overwhelming majority of plants, spirals were the basis of the position of leaves, and that the angles of divergence were rational parts of the circumference in the series of fractions $\frac{1}{2}$, $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$, $\frac{8}{21}$ . . . ., the law of which is at once evident, since every succeeding member originates from the sum of the numerator and denominator of the two preceding members. In all these spirals it naturally holds, since the angle of divergence is a rational fraction of the circumference, that, after a certain number of leaves, one will again be exactly vertically over the first leaf. They found a number of other laws for the sequence of the individual spirals of the same axis, as well as on different axes of the compound plants; at the same time they observed other aberrant conditions, which were neglected, partly as exceptions, partly as independent occurrences, in turn, of a peculiar regularity. The brothers Bravais started from the consideration of a mathematical spiral described about a cylinder, investigated the laws of position of points marked upon this at equal distances, and of deviations from them, when the distances of the turns of the spiral decreased and increased, when the cylinder was supposed to be an acute or obtuse cone, when a plane or concave surface. Then they sought to apply the laws thus found to actual plants, in instituting a multitude of very accurate and well-imagined measurements, defined the limits of error in these measurements, and finally showed that there was nothing to oppose their assumption of a single constant angle of divergence for all spirals, since the deviations of Schimper and Braun's discoveries fell within the limits of the possible error in the measurements. On account of the irrationality of the angle of divergence to the circumference here, no leaf ever stands exactly vertically over another throughout the whole axis. The spiral is from its nature infinite, and only comes to a termination by cessation of growth of the axis. Under this law they include all the cases of Schimper's series, above given, and many others besides, which Schimper could only take cognizance of through the assumption of a different kind of regularity. They call these leaves curviserial (*feuilles curvisériées*). Beside these remains a series of different cases, in which the leaf undoubtedly stands perpendicularly over a preceding one; these they call rectiserial (*feuilles rectisériées*), of which they have not yet given their development of the laws: they intimate, however, in their published views, that transitions from one system to the other occur, from whence it may be concluded that perhaps both may admit of deduction from one law.

Neither of the theories as yet possesses a safe foundation, since both regard only the developed plant, instead of tracing the course of development. The developed plant does not present itself as a mathematical body, and none of its leaves exhibit a mathematically equal divergence; we cannot come to the point here without a certain amount of *setting right*, and the admission of a pretty wide margin for errors of observation. The brothers Bravais say themselves, mathematical accuracy is almost superfluous in such researches, which admit of it so little; but they are certainly too good mathematicians not to admit, that mathematical laws which are not true to the hair's breadth are good for nothing. On the other hand, the history of development would of course place in our hands the power to find the mathematical laws confirmed with perfect exactness by experience. It only needs to observe the leaf- and flower-buds of *Coniferæ*, *Synanthereæ*, &c. beneath the microscope, to be astonished at the elegant and exact regularity which they here so strik-

ingly exhibit in their rudimentary condition. Here careful preparation and well-directed manipulation will safely admit of the measurements, which must confirm the laws with complete exactness, or overturn them. Moreover, the history of development alone can decide whether or not an abortion has ever occurred, which expedient in particular the brothers Bravais, like the whole French school since De Candolle, use rather too liberally. Finally, the whole matter can only acquire especial importance in botany, when we are in a condition to show, in the nature of the plant, the cause why the leaves arrange themselves in a certain spiral, why necessarily in this, and why they deviate therefrom under certain conditions. Then will the matter first come forward as something actually appertaining to the nature of the vegetable organism, since, for the present, we really possess nothing but the examination of the nature of the spirals in general, and the demonstration that, under certain presuppositions, these laws found for spirals admit of confirmation in the position of leaves.

Setting aside this want of more complete scientific establishment, the theory of the brothers Bravais is undoubtedly far preferable. Above all, the simplicity of the law is made good, and, according to a sound method, that mode of explanation is always preferred, which, under equal possibilities, traces back the greatest number of cases to a single point of view. Under these circumstances, perhaps, Bravais' theory may even indicate how, one time or other, the regularity of the position of leaves may possibly be deduced. If we recollect the well-known fact, that the usually greater development of root, on account of better soil on one side of a tree, also corresponds to a stronger development of the annual rings and branches on this side, — if we bear in mind the so frequently isolated course of vascular bundles, which, in that case, indicate the path of the influx of sap from the root to the leaves, — it seems to follow from this, as from a regard to what has been stated generally above in reference to the independence of the vitality of the cells, that also the separate perpendicular portions of the axis, lying horizontally side by side, have on the whole little influence upon each other, and are tolerably independent in themselves. If, then, the greatest possible number of leaves be placed upon the axis, and their most uniform possible distribution round the whole periphery, and thence the most uniform possible nutrition be effected, two leaves, one following the other, must necessarily have the greatest possible, and, in relation to the circumference, irrational angle of divergence, which demand the angle found by the Bravais, 137° 30′ 28″, completely answers. Of course this is at present but a teleological ground of explanation, but such an one may serve until a better, and the true one, be found, and it may even be the index pointing where to seek the truth.

Since the buds become abortive much more readily than the leaves, and often become quite displaced from their natural position by unequally rapid maturation, the application which both the German and French *savans* have made of their views to the inflorescence, seems to me to be so much the less admissible, in the entire neglect of the history of development at present, that it does not recommend itself by simplicity, but even deters us by a rather complicated terminology. I will not by any means assert that the authors have not succeeded in many instances in interpreting nature correctly, but they have neglected the only possible and accurate foundation — the course of development; and, therefore, there is too great a danger, in accepting these doctrines, of introducing something perhaps wholly false into science.

More details will be found in the following works: —

Dr. Schimper, Description of *Symphytum Zeyheri*, &c., in Geiger's Mag. für Pharmacie, B. XXIX. p. 1. et seq.

Dr. A. Braun, Comparative Researches into the Arrangement of the Scales in the Fir Cones, &c. (*Vergl. Unters. üb. die Ordn. der Schuppen an den Tannenzapfen, &c.*) Nov. Act. Acad. C. L. N. C. T. xiv., vol. i. pp. 195—402.

Dr. Schimper, Essays on the Possibility of a Scientific Comprehension of the Position of Leaves, &c. (*Vorträge üb. die Möglichkeit eines wissensch. Verständnisses der Blattstellung, &c.*) Published by Dr. A. Braun, Flora Jahrg. xviii., No. 10, 11, 12 (1835).

L. and A. Bravais, *Mémoires sur la Disposition géométrique des Feuilles et des Inflorescences, précédés d'un Résumé des Travaux des MM. Schimper et Braun sur le même Sujet, par Ch. Martins et A. Bravais.* Paris, 1838.

III. The primary form in which the leaf makes its appearance is, as I have above stated, always that of a little conical body which is pushed out from the axis; its ulterior form depends entirely upon the arrangement of the newly originating, and the expansion of already existing cells, and the leaf is as little confined to a definite circle of forms as any other of the organs, except the seed-bud. It may be globular, ovate, elliptical, and prismatic, as well as filiform, strap-like, and flattened in its expansion, and, by the greater accumulation of the cells in the middle than on the borders, or more flattened mode of expansion in the middle than on the borders, the plane surface may also produce concave forms. The most striking forms of this kind are called pouches (*asci*), as in *Sarracenia, Cephalotus, Utricularia.* In all these forms occur the modifications mentioned in the general morphology; in the plane leaves, especially the divisions and slight indentations of the border. One of the most frequent forms, which is usually laid down as the normal form, is this, — the upper part is developed into a plane, the blade of the leaf (*lamina*), the lower into a filiform part, the petiole or leaf-stalk (*petiolus*), and in the latter may frequently be distinguished, still lower down, a somewhat thickened or expanded portion, a sheathing portion (*pars vaginalis*), with which the leaf partly or wholly embraces the axis. This latter portion is frequently, especially in compound leaves, swollen into a greater thickness (fleshy), and is then called the cushion (*pulvinus*) of the leaf or petiole. As a general rule, the flat leaf is so developed that its surfaces look more or less upward and downward, rarely so that its borders have these directions, so that the axis lies in the plane of the leaf, as, for instance, in many New Holland *Myrtaceæ.* It is very different from this when a flat leaf of the usual development makes a half turn on its base, so that its surfaces are thus also placed vertically, as, for example, in *Lactuca Scariola.* One condition, which has already been mentioned when speaking of the axis, occurs also in the leaf, and here becomes of much greater importance. A joint (*articulatio*) is formed rarely (or never?) in the Monocotyledons, frequently in the Dicotyledons, between the leaf

and the axis, in consequence of which the leaf is, after a certain time, thrown off from the axis, while in other cases it gradually dies and decays on the axis itself. This true articulation is often repeated in the continuity of one and the same leaf, either only so that a joint is formed between the petiole and the lamina (e. g. in *Citrus*, *Dionæa*), or in such a manner that in the flat sub-divided leaves (e. g. *f. pinnatisecta*, *palmatisecta*, &c.), every lobe is connected to the main body by a joint. These latter are called compound leaves (*f. composita*), and, according to the subdivision, digitate or pinnate (*f. digitata*, *pinnata*, &c.). The separate parts are named leaflets (*foliola*), and the part connecting all these is the common petiole (*petiolus communis*). The leaflets can of course assume all the forms of the leaf, in particular they may be again separated into lamina, petiole, and pulvinus. In some New Holland Acacias (e. g. *Ac. heterophylla*) the first leaves are compound; they gradually form fewer and fewer leaflets, till at last the part corresponding to the common petiole alone remains, which then appears as a perpendicular plate, and is called a *phyllodium*, to distinguish it from the other perfect leaves of the same plant.

Botanists who imagine that the object of Botany is merely the correct definition of many species for their herbaria, will blame me for superficiality and want of profundity, in that I have so briefly and roughly treated the forms of leaves, which are the most essential grounds for the definition of species. I cannot help this: I merely find in these, as it may happen, good and bad methods of nomenclature for various partly or wholly divided surfaces or borders, for filiform or solid forms,—nothing at all botanical, much less, therefore, the properly scientific part of botany. If a slender filiform leaf be called a petiole, I have no objection to it, if nothing else be called by this name but a stalk-like leaf; but when it is superadded that the lamina is suppressed here, this is unscientific and false: if a leaf merely developed into a plate be alone called *folium sessile*, there is nothing to be said against the term; but when, in addition, it is said that the petiole is abortive here, this is again pure imagination. Whence in all the world does it follow from the essence of a plant that a leaf must regularly consist of lamina and petiole? The entire method in use up to this time, of describing the leaf according to blade and stalk, and of reducing all other forms under this conception, might so far have value, if we would, from the analogy of zoology, hold by the most perfect form, in order to obtain a type, with which to connect all others as deviations; then, however, we must start from the compound leaf, as evidently the most perfect. But it is as false to call all deviations, abortions, and Nature's unsuccessful attempts at formation, as it would be ridiculous to say that in *Monas lens* the toes and nails, the cartilage of the ear, &c. were abortive. Expressions such as "Nature has here attempted, she has here deviated from her type," are altogether unscientific, and no better than childish anthropopathy. In *Mesembryanthemum*, for instance, Nature has not deviated from the type of leaf-formation, but her type is different here from what it is in other plants; each in its kind is perfect, attaining the grand purpose of all vegetable development, the development of the most manifold construction of form from the very simplest elements.

I must here particularly remark, that there is no sense in explaining the triangular leaves, e. g. in some species of *Mesembryanthemum*, as leaves originally plane, which were then folded back and grew together by the posterior surface, or in regarding the leaf of the Iris as one folded together on the upper face, and with the sides grown together. The only proof which could be given of this would be the history of development, and this shows that such folds and growings together do not occur, but that, formed originally like all other leaves, the latter leaf expands into a vertical plate, the former into a triangular one, and nothing more. Through nothing else whatever can natural laws be established, but we must trace back all forms to one, or rather deduce all from one. That assertion would have a meaning *only* under the presupposition of such a natural law. But the mere fiction of such a natural law may be unconditionally repulsed. According to a fiction of Link's, in the same way arbitrarily manufactured, the leaves of *Abies excelsa*, *alba*, &c. originate from two with the upper faces grown together, which one sees in the two mid-nerves projecting above and below. Truly *Abies pectinata* and *Pinus sylvestris* have an indication of two free, parallel, vascular bundles, but *Abies excelsa*, *alba*, &c. only of one, and in the latter the upper and under halves are of a totally different structure; finally, the history of development shows decisively that only one leaf exists here, and not two grown together.

I will add a few words respecting the pouches or pitchers which occur in *Nepenthes*, *Sarracenia*, *Cephalotus*, *Dischidia Rafflesiana* and *clavata*, *Marcgravia*, *Norantea*, *Utricularia*, &c. At present we have not a complete history of development of a single species. The researches which I made formerly into *Utricularia* unfortunately still remain very imperfect. The pouches apparently present three different types: — *a.* In *Sarracenia* it is the lower part of the leaf which exhibits a form resembling a cornucopia, while at the upper border runs out a flat expansion (the lamina of the leaf) separated from the pouch by a deep incision on each side. The lower half of the internal surface of the pouch is clothed with hairs, directed downwards; the upper part is smooth. In *Nepenthes* a pitcher-shaped structure is borne upon a long petiole, winged below, then often tendril-like, and carries upon its upper border an articulated (?) lamina, which originally closes the pitcher like a lid. The inner surface is clothed in the lower part with little papillæ of very delicate, succulent cellular tissue, while above the epidermis projects down over these like the eaves of a house. In both, the cavity is formed from the leaf in such a manner that the closed base of the pouch corresponds to the base of the leaf (*Sarracenia*), or lies quite close to it (*Nepenthes*). In *Dischidia Rafflesiana* and *clavata*, on the contrary, the opening of the pouch is turned towards the base of the leaf; *Cephalotus* appears to possess a structure similar to that of *Sarracenia*.* In all the plants mentioned the pouch constitutes the main body of the leaf. (Some have found pleasure in debating whether the lid in *Sarracenia* and *Nepenthes* is the blade of the leaf or not, and how the individual parts are to be traced back to the supposed normal leaf.) *b.* In *Marcgravia* and *Norantea*, on the other hand, according to Lindley, the pouches are formed by the stipules. *c.* Lastly, in *Utricularia*, many separate little portions of the greatly divided leaf unite to assume a very complicated form of pouch. Originally these form a little, shortly-stalked, somewhat cornet-

* I only know *Cephalotus* and *Dischidia* from descriptions.

shaped body, in the angles of the divisions of the leaves. In this little body are especially developed the under side and the inner border of the orifice (which does not increase much in size), so that the full-grown pouch presents itself as a roundish and somewhat laterally compressed body, which above is continuous by one angle with the stem, while the other exhibits an orifice, which forms a little funnel projecting inwards. The external orifice of this funnel is closed by a kind of beard growing on the upper border; the lower part of the internal surface of the funnel is clothed with elegant hairs of various forms, but very regularly arranged, while the internal surface of the pouch exhibits peculiar hairs, consisting of two cells, each running out into a longer or shorter arm.

In leaves, as in plants in general, all forms are possible, and almost all actually existing, strict stereometric forms excepted. The terminology depends either on comparison with mathematical figures, or with objects presupposed to be familiar in common life. We have no scientific rule for this, æsthetic tact alone must be our guide. But within the limits of certain vegetable groups, certain circles of forms do exclusively occur; and, under the guidance of accurate observation, we can here establish more definite modes of nomenclature, which, however, are only valid for these definite groups. But this belongs to special botany. Lastly, it is wholly useless to teach the learner all the individual expressions, since most of them, from the facts that they are merely figurative, and that their correct application depends upon the degree of tact of the individual, are differently explained and applied by almost every botanist. I have adduced a stupid instance of this in the first part, and hundreds of similar examples might be collected in reference to almost every plant from the definitions of different botanists, and there is nothing left for the student but, for every author that he wishes to use, to begin the whole matter over again, and learn what is the exact sense in which he uses the expressions.*

The most important point evidently would be the laying down of morphological laws for the development of the forms of the leaf on one and the same axis of one and the same plant, genus, family, &c.; but nothing has yet been done towards this. The following alone can be expressed in very general terms:—1. The forms of the leaf low down on the primary axis are the simplest; they exhibit gradually upward greater and more manifold combinations, and return finally at the extremity to greater simplicity. The secondary (lateral) axes usually begin in the same way with imperfectly developed leaves (scales of buds), the forms then becoming more complicated, and finally simpler again. The end of the axis is here always known by the inflorescence. Both in the primary and the secondary axes, the transition from the simpler earlier forms (the cotyledons and bud-scales) into the variously developed leaves, is sometimes sudden, and sometimes very gradual through a number of intermediate forms.

2. Leaves which are formed under ground are always more simple

* If we went through the works of our most important systematists, we should, perhaps, not find one single definition in which two different so-called technical terms are not applied to the same fact; and I believe that I am right in saying that all these Latin and corresponding German descriptive terms mark no clear, and, in particular, no *botanical*, definitions, but serve for description of his impressions, according to the choice and skill of each individual, as well as any others which he might select; and to fill books or lectures with German translations of these Latin terms is a most unconscionable waste of time.

than those produced upon the axis above the surface. The former have usually the form of scales or spines.

3. Leaves which bear leaf-buds in their axils are generally more varied in form than such (bracts) as bear flower-buds in their axils.

4. The forms of leaves on one and the same axis are commonly of similar kind, or pass continuously into each other, within the limits of one definite series. Yet there are some remarkable exceptions to this, as in some *Araceæ*, and especially in the *Cycadaceæ*. In these plants two forms of leaf occur regularly upon the same axis: in the *Araceæ* very short membranous sheaths alternate quite regularly with leaves having sheath, petiole, and lamina; in *Cycadaceæ* most of the leaves are mere broad fleshy scales, which are placed spirally round the thick undeveloped stem, but among these occur, at first isolated, in well-grown stems more frequently, the great, handsomely pinnate or variously divided leaves, which regularly continue the spiral, taking the place of those scales: the sheathing portion of these leaves corresponds exactly to one of the scales; instead of a developed petiole and lamina, the scale bears only a little slender process. Only through most superficial observation could Link have asserted that the leaves spring from the axil of a scale.*

IV. If we examine the cotyledon of most Monocotyledons we find that, in its gradual development, it completely encloses the terminal bud (*plumula*); indeed that the exceedingly delicate, soft cells of the two borders of it become in part so firmly united, that they may be regarded as grown together, only a little fissure, which exists in *all* Monocotyledons, remaining. In germination the developing bud has not room to protrude through the little fissure, so that it pushes the borders of it more or less forward, and then these appear as a peculiar appendage on the middle of the cotyledon, as a membranous expansion of the border of the lower part of the leaf, or as lobes on its base. Similar conditions also occur frequently in the later leaves. In the Dicotyledons, a like condition presents itself not unfrequently; either the borders become expanded like a membrane on the base of a petiole or stalk-like leaf, or the emerging bud lifts up a longer or shorter membranous sheath, or peculiar lobules are formed on the base of the petiole, sometimes assuming the form of leaflets, and even connected with the petiole by an articulation. In all cases, without exception, they are, from the course of the development, parts of a leaf developed principally at its base, and in their essential nature, wholly identical structures throughout all the *Phanerogamia*, though they may vary most abundantly in their appearance. They have acquired very different names, which have been created, partly merely for particular families, partly solely for particular foliar organs. In the Grasses these parts are called the ligule (*ligula*): in other Monocotyledons, sometimes *vagina stipularis*, if large and rising free from the lowest part of the leaf; *vagina petiolaris*, if small and showing itself first higher up the leaf: in the Dicotyledons *petiolus alatus*, *stipulæ adnatæ*, if on the margins of the leaf-stalk; *ochrea*,

* Wiegmann's Archiv, 1841, vol. ii. p. 372.

if sheathing, as in the *Polygonaceæ;* or stipules (*stipulæ*), if appearing like special leaflets stationed beside the base of the petiole; lastly, in the floral leaves, *fornix, corona, nectarium,* &c., as in *Lychnis, Boraginaceæ, Narcissus,* &c. They occur as stipules, especially in compound leaves, where, sometimes, they alone are developed into a flat surface, while the leaf itself merely forms a filiform process, e. g. in *Lathyrus Aphaca.* At the base of the leaflets of compound leaves also little lobes sometimes occur, which, perhaps originating in the same manner, are called stipelles (*stipellæ*).

The organs just mentioned are developed *last* of all the parts of the leaf, as follows from the regular development of the leaf, from the summit to the base, but which may easily be demonstrated by observation of any bud of a plant which has but any stipules sufficiently perfect to facilitate the investigation, as in *Rosaceæ*, e. g. *Sorbus aucuparia*, in *Leguminosæ, Ervum nigricans, Orobus albus, Lathyrus sphæricus, Pisum sativum* (plate 77. fig. 1. et seq.), *Robinia Pseudacacia, Psoralea affinis* and *fruticosa*, &c. Link* asserts the contrary, evidently because he has never minutely examined the development of a bud, otherwise such an assertion would be impossible. Subsequently, their development of course goes forward more rapidly than that of the other parts, and they not unfrequently envelope the leaf to which they belong, in the bud, this acquiring its relatively large size at a later period by the expansion of its cells. The terminology of the parts is quite endless, for every single variation in the perfect plant is marked with a new name, without regard to the nature and origin of the organ; nay, a different origin is sometimes designedly indicated by the name, where the most superficial investigation would have shown that only one and the same part was in question, e. g. *vagina stipularis* and *petiolaris.*† Fancy has also been busy here in filling up the vacuities, which no one had an inclination to explain by fundamental investigation Growing together of the stipules with the petiole, &c., are quite current expressions, but without the least meaning; there is no growing together in the matter: *petiolus alatus* and *stipulæ adnatæ* do not differ the least in the world from each other, beyond the so-called wings running out into a little point above, in the latter. Arbitrary playing with words without any scientific foundation, has here, as almost everywhere, made mere patch-work of the terminology.

If we trace the development of these parts in the most different families of Monocotyledons and Dicotyledons, we readily become convinced that all are really one and the same part,—a greater development of the lower portion of the leaf or leaf-stalk; and, indeed, in most cases, particularly distinctly in the Monocotyledons, on account of the position of the foliar organs in the developing bud, and the pressure thus exercised

* Elem. Phil. Bot. ed. 2. t. i. p. 465.

† Meanwhile, it is to be observed, that in some Monocotyledonous families two very different things are included under one name, as in the *Araceæ.* Here, e. g. in *Pothos*, it not unfrequently occurs that the leaves are developed quite differently, alternating regularly; one consisting of lamina, petiole, vaginal portion and stipular sheath; the succeeding one appearing as a mere thin membranous sheath, which is neither a stipular sheath nor a vaginal portion, but an exceedingly aberrant form of the whole leaf. The description of such a plant must therefore necessarily be *folia dimorpha, foliis inæqualibus, alternantibus,* &c.

upon the lower portions, in the Monocotyledons especially, on the vaginal portion of the leaf. A plant of the Oat may be examined just after germination. Here there is a lanceolate, somewhat fleshy leaf (*scutellum*, Auct.) (fig. 172. *c.*), a vaginal portion (*a* to *b*), which includes about a quarter of the whole length of the leaf, and the free border of this vaginal portion which is pushed forward (*ligula*, *b*) by the protrusion of the bud. With no imaginable pains can one discover a cause which shall exclude this entire organ from the definition of a leaf, or even make its foliar nature doubtful; and, disregarding absolute size, colour, and fleshy consistence, which vary so abundantly in all foliar organs, there is not the slightest distinction to be found between the cotyledon and the succeeding leaves of the Oat, in the form and arrangement of the parts. If the vaginal portion is shorter, the protruded border somewhat larger, the thing has quite a different name (*vagina petiolaris*), and yet is altogether the same: finally, if the vaginal portion is very short, and the protruded border very long, it must be called *vagina stipularis*, without anything different from the foregoing being signified. The last two parts are best found, in every possible state of transition, and with them the *petiolus alatus*, which is also just the same, in the families of the *Hydrocharaceæ*, *Araceæ*, *Scitamineæ*, &c., in which I have analysed a sufficient number of sources of development. In the bud, where the leaf is only a line, and the vaginal portion half a line long, there can be no doubt about the nature of the so-called *vagina stipularis;* but when the leaf with the petiole has become two feet long, the *vagina stipularis* is several inches long, and the vaginal portion, which unites the two, which has remained at only half a line long, gets wholly overlooked in the usual way of examining these things, and the petiole and *vagina* are taken for two wholly distinct organs. What I have observed in the above-named *Leguminosæ*, in *Rosaceæ*, *Polygonaceæ*, and some other families, leads immediately to the conclusion that the organs called the sheath of the petiole, winged petiole, ochrea, adherent and free stipules, in the Dicotyledons, are all various forms of one and the same part of the lowest portion of the border of the petiole or leaf, and again are wholly identical in nature and development with the parts named in the Monocotyledons. The so-called free separate stipules have no existence at all; and, just as in the *vagina stipularis*, their connection with the petiole is overlooked, because the little piece by which they are connected is so small in proportion to the whole leaf, and even to the stipule, that it falls quite into the background. But when the leaf is examined before its cells expand, in the bud, the point of union of the leaf and stipules forms so considerable a portion of the whole length of the leaf, that there can be no more doubt on the subject, that the stipule is a mere appendage of the border

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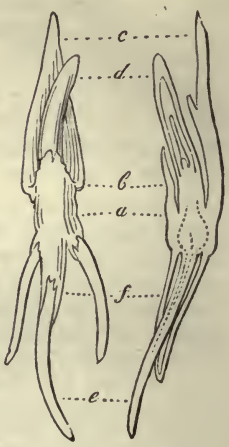



[172] *Avena sativa.* Germ plant, freed from the albumen, &c.; viewed in front (left fig.) and at the side in longitudinal section (right fig.). *a*, Body of the plant (stalk). *b*, *c*, Cotyledon. Between *a* and *b*, vaginal portion of the cotyledonary leaf; above this the ligule. *c*, Blade of the cotyledon. *d*, Outermost leaf of the bud, or plumula. *e*, Adventitious root, which breaks through the very slightly elongated radicle.

of the base of the leaf. The careful observation of the germination of a leguminous plant with greatly developed stipules would suffice to establish this opinion without any application of more fundamental researches into the course of development. For example, in *Orobus albus*, *Lathyrus sphæricus*, the first leaf after the cotyledon is a simply lanceolate leaf passing immediately into a broadly winged petiole. The second leaf is somewhat longer, yet still simple, and the two appendages adhering to the sides of the petiole must be called stipules; the third leaf is tripartite (*f. trifidum*), with stipules, the connection of which with the petiole still appears very considerable; lastly, the fourth leaf is a compound leaf with two leaflets, a terminal point and stipules, the connection of which with the long petiole is in proportions almost too slight to be noticed. The condition is similar in *Pisum sativum* (Plate III. fig. 1.), and everywhere; and from this alone it may be seen that *petiolus alatus*, *stipulæ adnatæ*, and *stipulæ liberæ* are one and the same part in different degrees of development. The same gradual development occurs in most buds; and, for instance, in *Prunus Padus* the leaves of the bud run through exactly the same series of forms from below upward as the germinating *Leguminosæ*. If this had been looked into, more than half of that terminology would have been wholly superfluous, even for Descriptive Botany, if, as a general rule, all those processes which go off, not merely from the borders, but at the same time from the surface, of the leaf, were called *ligula*; all distinct appendages of the border, *petiolus alatus* (e. g. *stipulæ adnatæ*, *lanceolatæ*=*petiolus alatus*, *alis lanceolatis*); finally, all parts which appear to be entirely free, *stipulæ* (e. g. *ochrea*=*stipula vaginans*), &c. In all these there are many further investigations still to be made, since, when I can even say that I have minutely traced the development in some fifty plants, this is far too few to carry back the so various phenomena, with complete certainty, to their fundamental structure; and there are still many families remaining in which I have not hitherto had opportunity to examine any plant. A large field for inquiry is especially left in the related parts of the floral leaves. In *Lychnis* the course of development, in *Narcissus* both this and monstrosities (e.g. the double *N. poeticus*), show that this part exists as *ligula;* wholly similar results may certainly be expected for the *fornix* of the *Boragineæ*, and other similar phenomena. Lastly, the nature of *stipellæ* has yet to be cleared up by the history of their course of development.

V. Every leaf, as already observed, originates as a little conical papilla at a definite point on the circumference of the axis. Even the sheathing leaves are produced in this manner, and at the point which corresponds to the middle line (the mid-nerve) of the future leaf by degrees, and as it is pushed up further from the axis, the parts of its circumference take part more and more in the development, and thus the base of the leaf gradually becomes broader, until it completely surrounds the axis. If the development of cells, or the expansion of existing ones, continues on the borders of the base of the leaf, beyond the degree required to surround the axis, the newly-formed, still soft and almost gelatinous cells of the two borders of the base of the leaf become applied upon one another, and become united as firmly as the cells of a continuous tissue; in this way the lower part of a leaf then becomes a closed, undivided

whole, surrounding the axis. If the lateral production of cells is small, and the union takes place relatively early, this closed portion forms a longer or shorter sheath, closely embracing the axis (*vagina clausa*), as in many Grasses. If, on the contrary, the lateral cell-production or expansion is considerable, and occurs relatively late, so that merely the base of the leaf forms a flat projecting border round the axis, the leaf is said to have the stem growing through it (*folium perfoliatum*), e. g. *Bupleurum perfoliatum.* When the axis is angular, and produces thin, more or less projecting plates upon these angles (the so-called winged axis, *axis alatus*), a similar process may enter into the bud in such a way that a flat leaf is connected at its base with the simultaneously-developed wing or angle of the axis, so that the full-grown leaf appears to be directly continuous with this. Such a leaf is said to run down the axis (*folium decurrens*), e. g. in *Carduus*, or, by a wholly unfounded fiction, a leaf blended by growth with the axis (*axis folio adnatus*). Where several leaves arise simultaneously, or almost simultaneously, at about the same height upon the axis, the bases of the leaves become gradually approximated during development; and here it may readily happen that they approach so close that the same process occurs between the bases of two different leaves, as has been already described in the two borders of one and the same leaf. Thus it happens, then, that leaves, which in their origin and at their summits are free and isolated, in their ulterior development and at their bases form an undivided whole (leaves grown together, *folia connata*). The leaves of *Lonicera Caprifolium* afford one of the examples simplest and easiest to trace. Two foliaceous organs which originate one above the other on the same axis (e. g. petal and stamen), or a leaf and the bud developed in its axil (e. g. the bract with the flower-stalk in the Lime), may grow together one above the other, in the same way.

Lastly, a process almost diametrically opposite to this may occur, where, namely, a leaf is developed, but becomes suddenly arrested in its development in a way yet unknown, whether through mere mechanical pressure or some other cause, by the more rapid and powerful development of the contiguous leaves; so that either the little original papilla escapes notice, on account of its relatively minute size in the full-grown part, or the little prominence actually becomes effaced by the subsequent development of the part, or, finally, the little rudiment of a leaf dies and gradually decays. In this case the leaf is said to be abortive: an instance easily traced is afforded by the third perigonial leaf of *Carex*, which aborts in this way, while the two others form the so-called *utriculus.* And not only may whole leaves become abortive in this way, but even individual portions of a leaf of which the rudiments already exist: thus it is not at all rare for the so-called stipules to become disproportionately developed in the rudimentary leaf, while the proper leaf, restrained in its growth, gradually disappears from sight. The bud-scales (*ramenta*) on the perennial buds of *Corylus avellana* may serve as

examples, being in fact nothing else than the stipules of an abortive principal leaf.

Finally, the same influence to which the parts closely crowded in the bud are subject, may merely cause the unsymmetrical development of the two halves a particular foliar organ, so that one side, or that part of the leaf lying on one side of the mid-nerve, assumes a form different from that of the other half, of which the species of *Begonia* afford a striking example.

The processes of development sketched here are the only ones in the life of the plant to which the words "growing together" or "abortion" can be applied, if we would confine ourselves within the boundaries of a circumspect, scientific activity. "Growing together" only has a meaning when I apply it to the union of two originally actually distinct parts, in consequence of a process of growth; "abortion" only when I understand by it the arrested development and destruction of a part already actually existing in a rudimentary condition. Nothing, certainly, has confused or led botanists more from their point than the misuse of these two words. That many take it to be much easier to build fancies about a phenomenon according to an arbitrarily chosen type, and to settle the question by a word thus thrown in, than to be compelled to see, after weeks and months of painful investigation, that their so beautifully imagined type is nothing, I readily believe; but must nevertheless assert that in the latter alone lies genuine scientific activity, while the former are toys of such who neither do nor wish to understand that the aim of our endeavours in Natural Science, is a theory of the actual and not of our imaginations. The misuse also depends altogether upon an empirical and methodical faultiness,—upon an empirical, in so far that we are yet wholly without the facts on which to establish scientifically a law of the position of leaves for Phanerogamic plants in general, as for the individual groups, while abortion and growing together can, in any case, only be used for the explanation of exceptions to a well-grounded law; upon a methodical, since an observed regularity may indeed serve in many cases to make us remark upon the possibility of a natural law lying at the bottom of it, but still is not the law itself, the actual existence, much more the decision, of which is then first to be sought for and established.* Here we have the misuse of the comparative method, on which I have before animadverted. If we find five leaves in a definite position in definite order in a series of plants, and in another plant, allied in many respects to the former, only four, comparison will of course lead us to guess that one leaf is abortive here, and call upon us to investigate; but it is this very investigation *alone* which can decide as to actual abortion. Any other mode of inquiry is as impossible as it would be unscientific. The individual case would have to be excluded if, in mathematical development from constituent metaphysical principles, we could deduce a law according to which exactly five leaves must stand in this position, where then the necessity conditioned by an exceptionless mathematically definite law would suffice to establish the decision; "for this appearance a leaf *must* have been obliterated here." We have no such laws at all in our

* See, on this head, the excellent elucidations of Fries, Versuch einer Kritik der Principien der Wahrscheinlichkeitsrechnung, Brunswick, 1842.

natural science, except in the pure study of motion, least of all in the barren, empirical beginnings of our Botanical efforts.

### b. *Structural Condition of the Foliar Organs.*

§ 132. 1. The nascent leaf consists, like all nascent parts of vegetables, of cellular tissue; determinate cords of cellular tissue are first gradually organised into vascular bundles, and in fact this process proceeds from the vascular bundles of the axis, and advances gradually into the leaf. In many foliar organs, especially the parts of the flower, no vascular bundles are ever formed. The vascular bundles of the leaves are distinguished by the most inconveniently chosen expressions, nerves or veins (*nervi*, *venæ*). In Monocotyledons with undeveloped internodes, the whole of the vascular bundles together (?) of the internode bounded above by the leaf, pass into the leaf. In all other plants, many at least of the vascular bundles entering the leaf are minor twigs of the vascular bundles of the axis; in the Dicotyledons proceeding exclusively, in great part, from the borders of the loop of the vascular bundles of the axis. The course of the vascular bundles in the leaf depends essentially on the form of the latter. In flat leaves, petioles, or vaginal portions, the vascular bundles lie in one plane; in relatively thick leaves, &c., they lie scattered (Palms) or in a circle (species of *Alöe*, *Mesembryanthemum*). The vascular bundles rarely run separately through the whole leaf (as in the last named): they mostly anastomose in various ways with each other by lateral branches; frequently in the petiole, in such a manner that all the vascular bundles entering it unite into a single one, and then separate again in the blade of the leaf. The form of the combinations is very varied: in many Monocotyledons the branches are short, going off at right angles; in others, and in most Dicotyledons, more varied, so that a net with polygonal meshes is formed.

De Candolle*, in particular, has devoted great pains to tracing up the distribution of vascular bundles in the leaf to certain types, and to the application of these to the division of plants into definite groups. I cannot perceive any regularity in it. The mode of distribution is as manifold as the form itself of the leaf upon which it is dependent, although De Candolle strangely takes the matter in the opposite way. The nearest allied plants often exhibit a different form of leaf, as also wholly different modes of distribution of the vascular bundles, e. g. *Alisma natans* and *Plantago*, *Funkia* and *Hemerocallis*, *Hydrocharis* and *Vallisneria*, *Taxus* and *Salisburia*, *Dortmanna* and *Isotoma*, *Sedum* and *Bryophyllum*, *Peireskia* and *Opuntia*, *Salicornia* and *Beta*, *Dianthus* and *Lychnis*, &c. No general laws, therefore, can be deduced from these facts, although it is right and useful most minutely to investigate and characterise the individual groups, families, genera, and species, in this respect as in all others. In many flat leaves we may distinguish one principal

* Organographie végétale, vol. i. p. 289, et seq.

nerve traversing the middle line of the leaf, and principal lateral nerves passing off from this. According as the latter make an acute angle, or are convex, toward the central nerve in their departure from it, De Candolle* distinguished *folia angulinervia* and *curvinervia;* the latter he claimed for the Monocotyledons, but they also occur frequently enough in Dicotyledons. When, on the other hand, the leaf is traversed by several equally strong nerves starting from its base, De Candolle called it *folium rectinervium.* These principal divisions were then further subdivided. Others, for instance Link and Lindley, have other divisions, because they make the principal distinctions depend on other forms. These various, equally valid, opinions, show that there can be no law here. These conditions are also quite inapplicable to the characterisation of plants and vegetable groups, excepting in isolated cases, where certain conditions are constant within the limits of certain groups, e. g. in *Melastomaceæ, Scitamineæ,* &c., which, on the whole, are very rare.

2. The vascular bundles of the leaves are progressive bundles, and they are so formed that (regarding the leaf as passing off horizontally from the axis) the oldest parts lie above, the youngest below. In the lower part also a cambium layer exists in the Dicotyledons; in the lower part liber-bundles accompany the vascular bundles, and in the under part the vascular bundles, in relatively thin and flat leaves, project above the surface (probably in consequence of gradual development), while the upper part of the leaf appears level.

We are at present wholly destitute of investigations into the development of the vascular bundles in the leaf, and need more minute observation of the condition of the unlimited bundles of Dicotyledons, and their condition in lengthened duration of the leaf. In *Pinus* and *Abies* I believe that I have been able to distinguish, in leaves two years old, two layers of the vascular bundle (similar to the annual rings).

3. The parenchyma of the leaf is developed in the most varied manner; in general, in thick, solid leaves, it is composed externally of small crowded cells containing more chlorophyll, internally, of larger and looser cells filled with aqueous juices. Very often the outer layer passes into a tissue, the cells of which are elongated in a direction vertical to the surface of the leaf, are applied closely, almost without trace of intercellular passages, and thus are pretty sharply distinguished from the rest of the parenchyma, and occur in the whole of the periphery of the leaf, not only in round and triangular leaves, but also in flat ones, as in many New Holland *Myrtaceæ.* In flat leaves, especially of Dicotyledons, there is very often a separation into two layers, the upper of which has the cells elongated perpendicularly to the surface, as just mentioned, filled with much chlorophyll, while the lower is composed of looser, globular, or, still more frequently, spongiform parenchyma containing little chlorophyll. In thick coriaceous or fleshy leaves, for instance, in species of *Ficus* and *Peperomia,* one or more layers of cells containing little

* Loc. cit.

but watery juices, often lie between the upper layer and the epidermis: more rarely, in like manner, at the under surface of the leaf.

Besides these, there appear at given places, or dispersed in the parenchyma, according to special peculiarities of the plant, spiral fibrous cells, very thick, and closely porous cells, and cells containing peculiar juices and crystals. We find also milk-vessels and passages, receptacles for gum, oil, and resin, also isolated liber-bundles, the last especially in the thin elongated leaves of Monocotyledons. Air-canals and air cavities are also found in the leaves; the last very regularly and beautifully arranged.

Here it is almost as difficult as in the axis, to make any general statements. Almost all combinations of forms of the elementary organs, and of the several tissues, are presented in the leaves; and much confusion has arisen from the attempts which have been made to seize arbitrarily upon some conditions, which, though frequently exhibited, are not invariable, and to assume these as the type from which all deviations are to be regarded as exceptions.

Let but the leaves of the *Orchidaceæ* be subjected to a complete and close investigation, and such a multiplicity of combinations will be discovered, that the attempt to account for them all by laws will be quickly laid aside. The *Aloineæ*, *Crassulaceæ*, *Ficoideæ*, *Piperaceæ*, *Proteaceæ*, and others, afford similar examples. In many plants we certainly find that division into a parenchyma more elongated, dense and green; and one expanded in all directions, looser and paler, strongly marked; but there are innumerable plants in which this is not the case in the Dicotyledons, but particularly in the Monocotyledons: hence it is altogether wrong to assume it to be the regular structure of the leaf. This too could only be done by assuming, in an equally arbitrary manner, that the flat leaf is the regular form. Amongst specialities, which cannot be brought under the general laws, may be enumerated the following: the frequent occurrence of spiral fibrous cells in the leaves of the *Orchidaceæ* of the tropics, and in *Gesnera latifolia*;* — the same in the stipules of the *Paronychiaceæ*; the peculiar stellate hairs which are projected into the air canals of *Nymphæa*, *Nuphar*, *Euryale*, &c.†, the similar very singular layer of clavate, sometimes ramified, and greatly thickened cells, traversing the layer of elongated parenchyma in the species of *Nymphæa*, *Nuphar*, and *Hakea*; — the thicker or thinner layer of almost colourless cellular tissue, which covers the layer of elongated cellular tissue in many species of *Peperomia*, and some of *Ficus*, whilst plants nearly related to them present nothing of the kind; the monstrous crystals often extending almost through the entire thickness of the leaf in the *Agaves* and in *Pontederia crassipes*; the cells often projecting into the air-canals on both sides of the septa containing bundles of crystals (Turpin's *biforines*) in *Aroideæ*, single large crystals in *Pontederaceæ*, or groups of crystals in *Myriophyllum* and *Proserpinaca*; the air-canals often arranged with such elegant regularity in water and bog plants; and the air cavities in the leaves of the Grasses‡, &c.

* But in none of its allies which I have been able to investigate. Here we may most easily trace the gradual conversion of true spirals into porous structures with slit-like pores.

† In a similar strange manner, also, in a rhizome of *Rumex crispus* (?).

‡ Even in the very young leaves of the group we find very delicate transparent

When milk-vessels are present, they for the most part follow the vascular bundles, lying on their under side; yet isolated milk-vessels are to be found dispersed through the parenchyma. If we compare the development of the vascular bundles of the leaves with those of the axis, we shall find, as the natural connection of the leaf and axis indicates, that the under surface of the leaf corresponds to the bark; and, agreeably with this, we find at times the external layer of bark extending out for some distance into the leaf.

We have little to say respecting the structure of the pouch, for investigation is yet wanting to us here. In *Nepenthes*, as in many other plants, the walls of the pitcher contain a large number of fine spiral fibrous cells. In *Utricularia*, the intercellular spaces in the walls of the pouch are strikingly large, and would be open, both internally and externally, were they not always closed by one or two cells, like a stopper, which bear upon their inner side peculiar four-armed hairs, and upon their outer one or two plano-convex cells.

4. All foliar organs, soon after their origin, exhibit a delicate epithelium, which, in plants vegetating under the earth or under water, is converted in time into epiblema, and in those vegetating above the surface is converted into epidermis. Some parts of flowers are clothed with a peculiar sort of covering, holding an intermediate station between epithelium and epidermis. We shall have subsequently to speak of this. To the epiblema stomata are wanting. The epidermis is commonly provided with them. In flat horizontal leaves they are very frequently wanting on the epidermis of the upper side, and they are usually only found where a thin or spongiform cellular tissue is present beneath the epidermis; in floating leaves, on the contrary, the upper epidermis only has stomata, and through the upper layer of condensed elongated parenchyma, air-canals pass into the under and thinner layer of parenchyma; as occurs also in leaves that are surrounded with dense, elongated cellular tissue. All parts usually known as appendages to the epidermis are also found occasionally on the leaves: even the cork structure is sometimes found on the petioles of long-enduring leaves, as, for example, in some species of *Pothos* and *Ficus*, as well as on the leaves of *Crassula*, *Bryophyllum*, &c.

The cells of the epidermis are usually filled with a clear watery fluid, which on the under surface of the leaf is sometimes colored (red). They more rarely present crystals, and yet more seldom offer any peculiar matter, as resin, or the like. The form of the epidermis-cells is determined by the form of the leaf; long, slender leaves usually present their epidermis cells elongated in the same direction. The lateral walls of the epidermis-cells are often curved in the form of waves, but this peculiarity has been too little investigated to be explained at present.

On the structure of the epidermis and stomata, enough has been said in the first part. Respecting the occurrence of the particular appendages of

parenchyma, formed of large cells; and this is destined by its laceration to form the air-canals, e. g. *Arundo Donax*.

the epidermis, nothing is to be said in general terms, but that hairs are infrequent on the surfaces of leaves in Monocotyledons. It is, however, to be remarked, that the leaves in the bud are sometimes furnished with hairs, which on further development of the organ fall away, and leave scars which are sometimes mistaken for original peculiarities. *Nuphar luteum** offers an example of this. Hairs consisting of a cylindrical cell, bearing a spherical cell above, and attached upon little indentations in the epidermis which they almost cover, are still more frequent: these also are frequently destroyed, and leave deceptive scars behind. The epidermis in their vicinity always presents some peculiarities. Of this the generality of tropical *Orchidaceæ* (*Pleurothallis ruscifolia*), and many of the *Piperaceæ* (*Piper obtusifolium*), are instances. As has been mentioned under the subject of the epidermis, some leaves present peculiarities in the stomata. In *Nerium*, *Banksia*, and *Dryandra*, small pits clothed with epidermis, beset at the edges with hairs, are found upon the leaf, and it is only at the bottom of these pits that the stomata occur. In *Saxifraga sarmentosa* and *cuscutæformis*, the stomata are ranged in groups, and they are set closely together. The longer diameter of the stomata is sometimes turned in one way, sometimes in another. In leaves proportionally very long, it is parallel to the longer diameter of the leaf, as in Grasses (*Liliaceæ*, *Coniferæ*). In some leaves, and especially in fleshy ones with leathery integument, the peculiar layer of secretion assumes a very considerable thickness, and even causes the leathery consistence of the integument. This secreted substance is in rare cases of a very soft gelatinous nature, as in *Hydropeltis*. Some leaves, as, for instance, many of the species of *Saxifraga*, have at their edges small groups of very delicate walled cells, filled with opaque contents, over which the epidermis is never perfected, but persists in the original condition of epithelium. In these groups is secreted the great abundance of carbonate of lime which occurs in these plants.

I shall speak of the development of individual cells or groups of cells of the leaves into new plants further on, in connection with propagation.

### c. *Complete Review of the Foliar Organs.*

§ 133. The floral parts of a plant are here advantageously distinguished from all other foliar organs, and are termed flower-leaves (*phylla*), whilst other leaves are termed true-leaves (*folia sensu stricto*).

#### 1. *True Leaves* (Folia).

*A.* Seed-leaves (*cotyledons*), generally round or flat, fleshy, little divided, and never compound. (See under *Embryo.*)

*B.* Stalk or stem-leaves (*folia caulina* †). Their forms are very various, as has been shown in the foregoing paragraphs. Those immediately following the cotyledons are usually simple; the

* Wiegmann's Archiv, Jahrg. iv. (1838), vol. i. p. 51.

† The term is allowable here. As opposed to *f. radicalia* it has no meaning, since the root never produces leaves.

next more perfect; and again, as they rise into the vicinity of the blossoms, they become again more simple. Filiform leaves, or parts of leaves, when they twine around foreign objects, are termed tendrils (*cirrhi*), as in *Pisum, Clematis,* &c.; those which are stiff and pointed are termed spines (*spinæ*); very concave leaves that exhibit the form of a cup or pitcher are termed pouches (*asci*), as in *Nepenthes, Sarracenia, Utricularia,* &c. According to their various positions are again distinguished from the true leaves generally: —

*a.* Leaves of the inflorescence (*folia floralia*). Indistinguishable from the stem-leaves, but bearing in their axils a blossom or a simple inflorescence.

*b.* Bracts (*bracteæ*). Leaves different from the stem-leaves, and bearing in their axils a blossom or a simple inflorescence; for instance, the scarlet-red leaves of the *Salvia Horminum.* To these belong the *glumæ* of Grasses, which are simply two bracts (which have commonly no blossoms in their axils), and the leaves which surround the *capitula* of the *Compositæ.* A number of bracts, inclosing an inflorescence, are also termed an involucre (*involucrum*). The quickly-drying bracteæ of the *Compositæ* are termed scales, or chaff (*paleæ*), a word altogether superfluous.

*c.* Bracteoles (*bracteolæ*), distinct from the stem-leaves, and standing beneath the blossom, but upon its axis; for example, the two leaves under the blossom of the *Aconitum,* &c.

*C.* Bud-scales (*tegmenta*). The very simple, mostly membranous, and quickly-falling outer leaves of a bud which remains for a length of time unexpanded. (See hereafter, under the *Bud.*)

2. *Flower-Leaves* (Phylla). See the *Blossom.*

*A.* Perigonial leaves (*phylla perigonii*).
*B.* Sepals of the epi-calyx (*phylla epicalycis*).
*C.* Sepals (*sepala*).
*D.* Petals (*petala*).
*E.* Pseudo-petals (*parapetala*).
*F.* Stamens (*stamina*).
*G.* Pseudo-stamens (*parastemones*).
*H.* Carpels (*carpella*).

## D. Of the Bud Organs (*Gemmæ*).

### a. *Of Buds in general.*

§ 134. 1. The bud is the end of a main or secondary axis, as yet undeveloped, but capable of development. We may distinguish: 1. The terminal bud (*gemma terminalis*), the end of a developed axis, itself capable of development. 2. The axillary bud (*gemma axillaris*), the end, capable of development, of a secondary axis newly

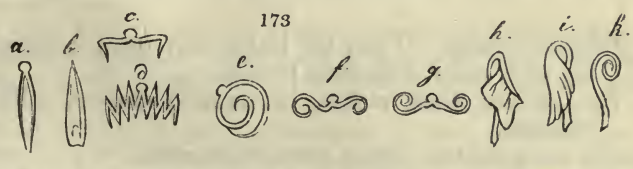
arising, according to law, in the axil of a leaf; since several buds may arise, without irregularity, in one axil, that which developes most vigorously is termed the main bud, the others accessory buds (*gemma axillaris primaria* and *accessoria*). 3. Lastly, the adventitious buds (*g. adventitiæ*), formed at the end of any (secondary) axis capable of development, arising irregularly on the plant. In all these we distinguish buds continually progressing in development (*g. vegetatione continua*); from buds whose vegetating activity rests for a time after their development into a bud (*g. vegetatione interrupta*).* Again, buds are distinguished into those which, in the natural course of vegetation, separate themselves from the parent plant and become independent plants (*g. plantiparæ*), and those which always remain in connection with the parent plant (*g. ramiparæ*). Finally, buds are distinguished according to their contents: there are the flower-buds (*g. floriparæ, alabastrus*); the leaf-buds (*g. foliiparæ*); and mixed-buds (*g. mixtæ*).

The bud is the yet undeveloped rudiment of the elongation of an axis already present, or for the formation of a new axis upon one already existing. Since it is not necessarily in the nature of Phanerogamic plants to bear true leaves, so it is not necessarily in the idea of a bud that it should contain the rudiments of leaves, much less that the rudiment of a leaf precedes that of an axial organ; therefore the youngest condition of a bud is merely one in which no rudiments of leaves exist. I have styled the axillary and adventitious buds *ends* of an axis capable of development, instead of describing them as the axis itself in undeveloped circumstances, for this seems to me a simpler and more universal definition; and the first origin of such bud appears to me to take place within the parenchyma, so that that which projects as the visible bud might, with equal right, be considered as the end of a particular mass of cellular tissue. I shall speak of the origin of the axillary and adventitious buds when I come to the subject of propagation. One peculiarity I must not omit here to mention, namely, the total absence of terminal buds, capable of development, in certain plants. This occurs without exception in the *Lemnaceæ*, whose flat stem never forms more than two axillary buds, and has no terminal bud. The same remarkable circumstance is observable of the stems of *Ruscus*, developed above ground, where every branch spreads out into a flat leaflike expansion, and terminates in a spine instead of a terminal bud. This holds for the short flower-bearing side branches, as well as for the thin, long, main branches, out of angles of the leaves of which those flower-bearing branches spring. This must not be confounded with those cases wherein a terminal bud is indeed originally presented, but is very frequently abortive, as in *Syringa vulgaris;* nor with those where it is always developed as a flower-bud, as in *Viscum album.* The accessory buds so frequently occurring in the axils of leaves (see Rœper in the Linnæa, vol. i. p. 461.), for instance, in *Aristolochia Sipho, Gymnocladus canadensis,* &c., certainly merit a more minute investigation of their development; they may of course often merely represent collectively the secondary axillary and terminal buds of a solitary, the proper primary axillary bud, for instance, certainly in *Cornus mascula, Ptelea trifoliata, Salix capræa,*

* Which Linnæus called *hybernacula.*

and the *Malvaceæ;* in other cases it is at least probable, as in *Aristolochia Sipho,* though in others, at least in the perfect condition, highly improbable, as in *Gymnocladus.* Every terminal bud is but the progressively developing end of a simple axis, and may have unlimited growth; the only limits are found in the completion of the last foliaceous and axial organ into normal flowering parts, and apparently in the impossibility of further endosmosis and of further nourishment, when the terminal bud has become removed very far from its source of nourishment (the earth). That the first determination does not *necessarily* ensue at a definite epoch, on account of morphological laws of the elementary organs, is shown by continuance of growth through flowers; that the second limitation of the longitudinal growth is an external one, is demonstrated by the possibility of producing longitudinal growth in the utmost extremities of an old stem by making slips of them. Links's distinction between closed and open buds is quite useless; *all* buds are originally closed; *all* buds are open during development. The only cases in which such distinctions can apply, are when they develope immediately, and when they remain closed for some time.

2. With the exception of the true tuber in *Solanum* and *Helianthus* (?), and of the tuber buds (*tubercula*), all buds have a determinate number of rudimentary foliar organs. These foliar organs are folded in specific ways (*vernatio*), and have a definite position in relation to each other.* From the origin of the foliar organs, it follows that when several arise at the same height, they will always be at some time in such a position that their edges will be in contact (*vernatio simplex, foliatio valvata*).† This position often persists during the whole period of the bud remaining as such; it is, however, changed by various circumstances, not yet clearly understood, but which appear to be caused by the individual development of the separate leaves. In the *vernatio* the following main forms may be distinguished: the foliar organs are either curled up in the direction of their length or their breadth, or they are compressed together in irregular folds (*vern. corrugativa*). In those leaves that are curled up lengthways, we distinguish sharp folds from those which make rounder curves.




* Linnæus used the expression *foliatio* in the way I do. Subsequently, and unnecessarily, the words *præfoliatio* in the leaf-buds *præfloratio* in the flower-buds, were substituted for *vernatio* and *æstivatio.* I here restrict *vernatio* in the manner stated. The matter required a name, and that word already exists. But, at the same time, we have here an example of the completely unscientific character of terminology. The four last terms are altogether superfluous, since in this condition it is all one whether the foliaceous organ be modified or not. On the other hand, the folding of a single leaf by itself, and its position in relation to others, which are clearly two very distinct things, are called by the same name.

† When there are only two leaves, a superfluous term, *foliatio applicativa,* is applied.

*A.* Sharp folds.

*a. Vernatio duplicativa.* Simply folded together (forwards) upon the upper surface of the leaf, as in *Quercus, Tilia,* and the *lamina* of *Liriodendron.*

*b. Vern. replicativa.* Folded in the same way backward upon the under surface of the leaf.

*c. Vern. implicativa.* The two borders folded in sharply forwards, as in the perigone of *Clematis.*

*d. Vern. plicativa.* Many longitudinal folds, as is seen, though not quite perfectly, in *Fagus* and *Carpinus,* but better in *Alchemilla,* and best of all in *Panicum plicatum.*

*B.* Rounded folds.

*a. Vern. convolutiva.* Simply rolled up, as in *Calla* and *Prunus.*

*b. Vern. involutiva.* With both edges equally rolled up forwards, as in *Alisma* and *Populus.*

*c. Vern. revolutiva.* Rolled backwards in a similar manner, as seen in *Salix* and *Nerium.*

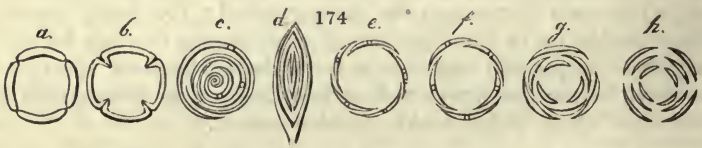
In leaves curled and folded together the cross way, the most important distinctions occur.

*a. Vern. inclinativa.* Incurved forwards, as in the petiole of *Liriodendron* and *Hepatica.*

*b. Vern. reclinativa.* Recurved backwards, as in *Aconitum.*

*c. Vern. circinata.* Rolled up forwards from the point to the base, as in *Cycas.*

In the *foliatio* we distinguish the position of the foliar organs in relation to one another, in general, from the position of individual circles of foliar organs with respect to each other. With regard to the first of these, the conditions have been pointed out.




*A. Foliatio valvata.* When the leaves only touch without covering each other with their borders.

*a. Fol. valvata sensu stricto,* in *vernatio simplex.* Flower in *Stapelia.*

*b. Fol. induplicativa* (?), in *vern. duplicativa.*

*c. Fol. implicativa,* in *vern. implicativa,* as in the perigone of *Clematis.*

*B. Foliatio amplexa.* When each leaf embraces all those within it.

*a. Fol. convolutiva,* in *vernatio convolutiva,* as in *Prunus armeniaca.*

*b. Fol. equitans,* in *vernatio duplicativa,* as in *Iris.*

*C. Foliatio semiamplexa.* When each leaf embraces with one edge, and is embraced on the other.

*a. Fol. contorta,* in *vernatio simplex* (more than three leaves), as in the flower of *Dianthus* and *Linum.*

*b. Fol. obvolutiva.* In *vernatio duplicativa,* as in *Lychnis.*

*D. Foliatio quincuncialis.* When five leaves so lie that between two external, quite uncovered ones, and two inner, quite covered ones, the fifth is so interposed as to cover one of the inner leaves with one edge, and to be covered at its other edge by one of the external leaves, as in the flower of *Rosa.*

*E. Foliatio connata.* When the leaves of a circle are so perfectly and intimately grown together that on the full development they become ruptured from their common basis, and fall away like a cap, as in some calices, for instance, *Eucalyptus, Eschscholzia;* and bracts, as in *Aponogeton distachyon,* &c.

Finally. In respect to the position of individual circles of foliar organs with respect to one another, the following have been distinguished: —

*A. Foliatio alternativa.* When the members of the one circle stand before the interspaces occurring between the members of another circle, as in the calyx, corolla, and stamina of *Lysimachia.*

*B. Foliatio oppositiva.* When the members of one circle stand before the members of another circle.*

From this review, arranged as logically as possible, it is evident at the first glance, that here, as almost everywhere, in the position of the foliar organs in the bud, the terminology has been patched together without the least reviewal and arrangement of the *possible* conditions, without complete investigation of the *actual,* and therefore altogether without any principles; just as one or other inquirer lighted upon this or that form, and gave it a new technical name, without reference to those already existing, and without any scientific relations. We are destitute, therefore, of certainly established technical names for some of the most important distinctions, and in other cases have a number of different words to express the same fact: such I have omitted, as altogether superfluous.

Some other words which are chosen to designate peculiar forms in certain plants of particular families are of no general value, and belong evidently to special descriptions of particular groups: such are *foliatio cochlearis,* in the flowers of *Aconitum* and *Lamium,* and *foliatio vexillaris,* in the flowers of the *Papilionaceæ.* I have retained Linnæus' term *foliatio,* by which to designate the position of the leaves in relation to each other in the bud, as being the oldest and best; and for the position of the individual leaves I have used the term *vernatio,* which was before superfluous, as a distinction between the two conditions is indispensable.

* Perhaps not actually existent in nature. Most of the instances which are usually brought forward, e. g. the parts of the flower of *Berberaceæ, Thymelaceæ,* &c., have only been included here, through superficial observation: in the former there are alternating 3-partite, not opposite 6-partite circles; in the latter, in like manner, 2-partite, not 4-partite circles.

3. Since in the uninterrupted development of buds they become axes and leaves, there is nothing general to be said further on the subject which has not been mentioned already under those particular organs. We must not, however, pass over buds with uninterrupted vegetation, since they appear to hold a place as a peculiar organ of the plant. In these we find that the external (undermost) leaves are modified in peculiar ways, their forms appearing simpler than those later developed (higher up) from the same bud. They may be termed in general bud-scales * (*tegmenta*), and, according to their various origins, *tegmenta foliacea*, as in *Fagus* and *Æsculus*; *t. stipulacea*, as in *Carpinus*, *Corylus*, and *Betula*; and, lastly, *t. vaginalia*, as in the bulbs of *Allium*, *Lilium*, &c. Again, there is an essential distinction between the propagative and branch buds: the first are developed in a very solid and fleshy manner, either in all their parts, as in the generality of bulbs and bulblets, e. g. in *Lilium candidum*; or in their axial organs, as in the true tubers, e. g. in *Solanum tuberosum*; or in the foliar organs, as in the so-called solid bulb of *Allium ursinum*; or, lastly, in certain determined parts of the axis, as in the European *Orchideæ*, and the Dahlias; but in the branch buds this fleshy development does not occur. On the other hand, in the development of the latter buds to branches their bud-scales fall away; but in the propagative bud they gradually die away from without inwards, and envelope the bud with a thinner or thicker layer of dry membranes.

Since it is most evident that bulbs are not roots, as many treat them, but buds, there is no reason why the term *tegmenta* should not be applied to those parts which, inasmuch as they are modified leaves, or parts of leaves, and have essentially the function of shielding and covering that part of the bud really capable of development, during the time of its rest from vegetation, are clearly morphologically and physiologically the same organs as the bud-scales. By applying the term *tegmenta* to these also, we divest ourselves of one useless expression in terminology, which is certainly a gain. *Perula* is a term wholly without etymological sense; and it is quite superfluous to discriminate between *tegmenta* and *ramenta*, since both are parts of a leaf, or, more correctly, imperfectly-formed leaves.

### b. *Structure of the Bud.*

§ 135. The structure of the bud has in part been sufficiently discussed in the examination of the axis and leaf, but the several peculiar kinds of bud require special treatment. We may, however, first make the general remark, that all buds consist originally

* Link's (Elem. Phil. Bot. ed. 2. vol. i. p. 467.) comparison of the bud-scales with the cotyledons is either very idle, if it means merely that both are foliar organs, like other leaves, or distinctly wrong, since the cotyledons have the function *solely* of nourishing the embryo, and the coats of the seed effect the protection during the rest from vegetation, while the *tegmenta* have only the function of protection. The nutrition is carried on by the axis on which the bud is situated.

of parenchyma with very delicate walls, and that the vascular bundles are subsequently prolonged in this: the thickening of the cell-walls begins in those cells lying adjacent to the vascular bundles of those parts on which the bud arises, and gradually proceeds into the bud.

So far as my observations extend, though they are, I must confess, insufficient, the conversion of the cells of the buds into vascular cells proceeds in all cases from the vascular bundles of the part on which the bud arises. But it is easy to be deceived here, since the parenchyma of the pith of the bud always is in continuity with the parenchyma of the part on which the bud arises, and since the vascular bundles going to the bud more frequently unite with the vascular bundles of the part forming the bud, at the sides than in the upper and under part (where, at least in axillary buds, the lower vascular bundles of the axis are received by the leaf), and therefore it is difficult to perceive the whole of the relations correctly in *one* section, particularly as it is necessary to go back to the very earliest condition. It is self-evident that the vascular bundles of the terminal bud are but a continuation of the vascular bundles of the axis. On account of the difficulty of this investigation, I by no means set up my observations as affording conclusive arguments against views opposed to them. I shall return again to this point when I speak of propagation.

### c. *Of the particular Forms of Buds.*

§ 136. *A.* Buds developing in uninterrupted vegetation. These may also be termed open buds, because they seldom or never exhibit a closed form, since in these the leaves are gradually developed to the perfect form and size, from the perfect rudiments contained in the bud. Yet in these buds the *foliatio* is always such, that the youngest and tenderest parts are defended from the influence of the atmosphere, and almost wholly enclosed.

In tropical Monocotyledons, such buds are presented, with few exceptions, only as terminal buds; in all other stems they are both terminal and axillary: in this case they approach most nearly to the closed buds of the following divisions. They occur also, though seldom, as adventitious buds on the stalks and on the stems of Monocotyledons and Dicotyledons, perhaps only in consequence of artificial means used thereto, by cutting or wounding the barks: as an example of this, I may name here the wounded stems of the species of *Dracæna* and *Cactus*, with neither of which, however, I had opportunity to convince myself fully, whether the developing buds were truly adventitious buds, or rather axillary buds coming into development, which, in Monocotyledons generally, especially on main stems, but also in most *Cacteæ*, persist for a very long time in the rudimentary condition.

*B.* Buds with vegetation dormant for a certain time.

#### 1. Buds of Shoots.

*a.* Terminal and axillary buds of perennial plants, with periodically dormant vegetation. Of these we are only intimately

acquainted with the native trees of our woods and forests. It is characteristic of these, that the young leaves, which subsequently come to perfection in the more developed axis, are enveloped whilst in the bud by stipules, which, soon after the development of their leaf, fall away (*stipulæ deciduæ*), as in *Liriodendron*, or in leaves or stipules of simple structure, of which the laminar portion is abortive (*tegmenta*): and there are varieties amongst these, so far that either only the external or inferior leaves, or stipules, appear as coverings of the buds, as in *Fagus;* or the coverings of the bud seem to be continued into the interior of the bud, but alternate with leaves capable of perfect development, which lie between and are covered by them, as in *Acer*. The coverings of the bud are for the most part tough, and almost leathery; they are often filled and coated over with resinous juices, and then mostly fall off in the development of the bud, but they also occur thin and herbaceous in texture, and even change quickly into dry thin membranes, which mostly remain upon the plant: these last are seen in *Pinus*.

The study of the bud is yet far from being complete: it requires much comprehensive investigation. The best works which we possess upon the subject are two essays of A. Henry.* But we want here the full history of the development, without which nothing important can be accomplished. The coverings of the bud are the undermost or inferior leaves of the bud which is developing to an axis; they are sometimes many, sometimes few. Sometimes the internodes between the deciduous (*Fagus sylvatica*) or persistent (*Abies excelsa*) bud-scales remain undeveloped. All (?) plants here referred to develope yearly only one simple bud, which was formed in the preceding year. A few plants deviate from this rule in a manner which, after Linnæus, may very properly be called *prolepsis*. This occurs in some degree in *Alnus*, in which the under-leaves of the axillary buds are developed in the same year that they are formed: hence the buds coming to development in the spring are properly only terminal buds. *Pinus* deviates from the rule in the most remarkable manner, in which all the leaves of the axillary and terminal buds, *gemmæ primariæ*, appear as bud-scales (*tegmenta primaria*), and in the next year, on the development of the bud, they fall away, all except one little scale†, whilst the already formed rudimentary axillary buds, (*gemmæ secundariæ*), which should only reach development in the third year, are now developed; on these secondary buds also the inferior leaves are membranous bud-scales (*tegmenta secundaria*); and only the two to seven of the upper leaves directly beneath the secondary terminal bud, which almost always remain in a most rudimentary condition, become developed into perfect leaves, and thus these, as the internodes of the secondary bud do not develope, appear to arise, from two to seven

* Nova Acta A. L. C. N. C. t. xviii. p. 1. and v. xix. p. 1

† This is then of rather tough texture, and is merely the lower (in the bud condition green) portion of the otherwise dry and membranous bud-scale. This is remarkable for an interesting structure. The cells are all elongated, and in the middle thickened by indistinctly porous deposits, almost to the filling up of the cavities. The cells of the margins, on the contrary, where the bud-scale appears lacerated, exhibit a very thin membrane, with a spiral striation of the utmost delicacy; and the cells, which appear on the border in the form of single hairs, tear, when pulled out, into a spiral band, just like the hairs of the *Mamillariæ* and *Melocacti*.

in number, and surrounded at the base by a membranous sheath, immediately from the branch on which the primary bud was developed. *Pinus* and *Abies* exhibit the further peculiarity that they develope two, three, or more primary axillary buds to true branch buds only at lengthened intervals; otherwise, in *Abies*, the axillary buds only exist potentially. In *Pinus*, as has been remarked, the leaves never form the end immediately continuing the axis, but between them is always found a very small rudimentary terminal bud, which is often merely indicated by a little flattened papilla composed of a few cells. Some botanists, and that even recently, have esteemed these leaves as a part of the divided axis; a view which does not involve an impossibility, since in the *Rhizocarpeæ* a ramification of the axis occurs without antecedent formation of buds, but which, in the way it was put forward, was a mere fancy, in which the question was not once examined by a thorough investigation of the fully developed parts, much less by a study of the course of development.

*b.* Adventitious buds of perennial plants, with vegetation periodically dormant. They are only distinguished from the foregoing by the mode of development. Each stem, whether a common one or a root stem, can develop a bud. These buds are caused, not only by accidental and intentional wounding of the stem, but also by the inclination of plants to develop buds at certain places. Many plants exhibit upon their bark peculiar little groups of lax, roundish cells, which originally lie under the epidermis, which, however, is soon destroyed above them, leaving them bare (*lenticellæ*). The result of this exposure is, that at these places the bark is rent by the distension of the bough or stem; hence the newly vegetating part of the bark comes in contact with the air. It is principally at the edges of the rent bark that the adventitious buds are found.

Link says (l. c. 337.), the adventitious buds are distinguished from the axillary buds by their structure; in the latter the greater part of the pith goes with the wood into the supporting leaf, and in the former the entire amount of pith passes into the bud. Accurate observation shows that the supporting leaf stands in no connection with the pith, and that from the wood into these only small vascular bundles enter; whilst, on the contrary, a thick cylinder of pith, and at a later period, a complete circle of vascular bundles, subsequently forming wood, enter into the axillary buds; and that further, the adventitious buds stand in no immediate connection with the pith, but only with the medullary rays; of this every twig of the Lime will afford an example.

Respecting the import of the adventitious buds, I shall have to speak again more fully when I come to the subject of reproduction. Here we have merely to state in general terms the cause of their origination. It is well known that injuries, such as the breaking or cutting off of a branch, usually call forth a number of adventitious buds. Very little, indeed, is yet known of the import of the lenticels in relation to this point. That these are not, as De Candolle* supposed, root-buds, Du Petit Thouars and H. Mohl (Flora, 1832, No. 5.) have proved beyond all question, and as every attentive observer is aware. I believe that I have obtained a pretty sure conclusion as to the import of these (perhaps a

* Organographie, v. i. p. 95.

very insignificant and accidental one), as above given, by close comparison of the shoots and stems of the Italian Poplar and the black Poplar through all their steps. My knowledge goes no further, and there is here again a hiatus, which certainly would have been partly filled up already, had the time spent in useless ratiocination and writing about these objects been rather applied to true investigation of nature.

### 2. Propagative Buds.

*a.* Bulbs (*bulbi*) are Monocotyledonous stems, with undeveloped internodes, which gradually die away from below upwards, and therefore remain always very short, with perennial leaves, whose vaginal parts die away and enclose as thin membranes, the sheaths of the inner leaves still living, and always fleshy and thick (bulb scales), or more rarely die away speedily and leave bare the latter, as in *Lilium.* They are formed either immediately from the embryo, and then the sheathing part of the cotyledonary leaf becomes the first bulb scale; or they are formed from the axillary buds of the bulb, or from the axillary buds of the stems which have sprung from the bulbs, as in *Lilium bulbiferum:* less frequently they are from adventitious buds on leaves or other parts. We distinguish:—

*A.* The leafy bulb (*bulbus foliosus*).

1. The tunicated bulb (*b. tunicatus*), where many sheathing parts are closed round, or embrace the axis pretty broadly, as in *Hyacinthus orientalis.*

2. The scaly bulb (*b. squamosus*), where many sheathing parts, relatively slender and short, are seated on the axis, as in *Lilium candidum.*

*B.* The solid bulb (*b. solidus*), when the bulb is formed of one single living sheathing part.

So far as my knowledge extends, no Dicotyledonous plant presents a true bulb, although there is nothing impossible nor improbable in such a thing; since if we disregard the character of the undeveloped internodes, and thus make the definition more general, the subterranean stems of *Lathræa squamaria, Dentaria bulbifera,* etc. are *bulbi squamosi.* I would, however, the less recommend such an innovation, since the discovery of a true Dicotyledonous bulb would make the definition proposed appear more to the purpose. Another question is, whether we shall reckon the bulbels of some of the species of *Oxalis* here. I have not myself found opportunity sufficiently to examine them, and therefore leave them for the present among Dicotyledonous bulbels, since I make the persistence of the bulb, as such, a character of its definition. On the other hand, it is quite incorrect to separate the axillary bulb of *Lilium bulbiferum* from bulbs: since it is a bulb in its structure, it always remains a bulb, and it is formed in the axil of a leaf of a bulbous plant, whether on the stem or the stalk, appears to be quite unimportant.

The three divisions of bulbs which we have given are practical subdivisions of bulbs, as such, according to their composition out of the parts necessarily present to make them fall within the definitions.

It is inconceivable to me how the reticular bulb can be arranged as A 3., simply because in some tunicated bulbs the external decaying coats become at last fibrous. If this mode of classification were correct, we

must, on the same principle, have class 4 brown, 5 yellow, 6 red bulbs, &c.; we must class others, as containing starch, or gum, because their inner scales sometimes contain starch and sometimes gum. In the solid bulbs we have also heard of blending of the coats of the bulb; a sufficient proof that no one had taken the trouble to analyse the well known examples of bulbus solidus, and to compare them together, much less thoroughly studied the history of development. Each germinating bulbous plant has, during the first year, a bulbus solidus (fig. 175.) on an infantine scale, because then only the thickened sheathing part of the cotyledonary leaf is present (fig. 175. *c*).

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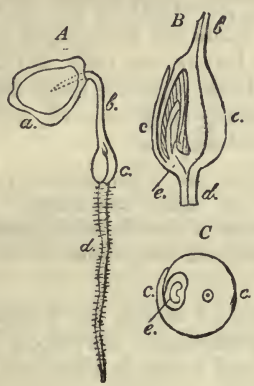


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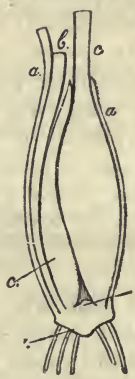


Whether a bulb shall later be known as bulbus solidus or bulbus foliosus depends upon the time required before the external sheathing parts begin to die away, and upon the greater or less mass to which the sheathing part enlarges. The distinction is not of vast importance, since in the same genus are found the leafy bulb (*Allium Cepa*) and the solid bulb (*Allium ursinum*) (fig. 176.). In families there is little or no constancy of this character. I have traced the history of the development of *Allium Moly, acutangulum, ursinum* (fig. 176.); *Gagea lutea, arvensis; Hyacinthus orientalis, Lilium pumilum* (fig. 175.); and *Tulipa sylvestris.* There is yet another point, which makes the precise definition of a bulb very difficult. If we compare the series of gradations of the bulb from *Allium Cepa* to *Allium Porrum*, and from this, through *Allium sativum*, to the common Monocotyledon bud, especially to that with uninterrupted vegetation, for instance, in *Phormium tenax*, it will be very difficult to draw a line of distinction, which indeed scarcely seems to exist in nature.

In treating upon axes and leaves, the most important matters con-

[175] *Lilium pumilum.* Germination. *A*, Natural size: *a*, seed; *b*, sheathing part of the cotyledonary leaf; *c*, the sheathing part exhibiting a small solid bulb; *d*, the radicle. *B*, A longitudinal section through the under part of the cotyledon, somewhat enlarged: *b*, *c*, *d*, as in *A*; *e*, the body of the plant (stalk), and foundation of the bud. *C*, A cross-section through the midst of *B*: *c c*, as before; *e*, the largest (external) leaf of the bud.

[176] *Allium ursinum*, natural size. A longitudinal section through the solid bulb. *a a*, Withered leaf, clothing the bulb as a membrane; *b*, flower-stalk; *c*, fresh leaf, whose sheathing part encloses the next year's bud (*d*), which is the terminal bud of the stem (*e*), which is continually dying away beneath.

nected with the structure of buds were discussed. There is little peculiar to the bulb. The epidermis of the bulb-scales in *Allium Moly* covers a cellular layer, flat cells of which exhibit the strangest and most irregular forms, and seem to be interspersed between each other, somewhat in the same way as the parts of the well-known child's toy, where a picture is glued upon thin board and sawn up into irregular, variously-shaped pieces, which fit into each other. These cells are thick-walled, and very porous. In *Gagea lutea* and *arvensis* a layer of spiral fibrous cells is found in the same part. In *Allium ursinum* and *Colchicum autumnale* I do not recollect to have observed this; nor have I seen it in any bulbs with many leaves.

*b.* Bulbels (*bulbilli*). To plants not perennial by means of a bulb (only Dicotyledonous?), the axillary buds are sometimes developed into bulb-like forms, in which the leaves are only developed as thickened, sheathing parts, and the buds separate from the parent plant by the dying away of the supporting stem or stalk, and become independent plants, as with *Dentaria bulbifera.*

From the want of personal investigation, and accurate ones from other quarters, I am unable to say much upon these structures. I cannot decide whether the bulbels of some species of *Oxalis* belong here. *Bulbilli* ought to be definitely distinguished from true bulbs, in the manner above stated.

*c.* Tubers (*tubera*). On underground stems the axillary buds (of attenuated scaly leaves) are sometimes developed in such fashion that the entire axis of the bud becomes thickened, fleshy, and of a knobby form; the leaves are quite in rudimentary condition, or scarcely to be recognised, whilst the axillary and terminal buds remain capable of development, and after the dying away of the stems of the parent plant form new stems, as in *Solanum tuberosum.*

The growth of the potato from an axillary bud of an underground stem is easy to trace (fig. 177.); and if we grow the potato in such a manner that a part of the bottom of the stem must remain above the surface of the earth (a circumstance which occurs continually with potatoes badly earthed up), we shall see all the stages and degrees which exist between a perfectly normal axillary bud and a normal potato. From want of the entire history of the development, I cannot here decide whether the tubers of the *Helianthus tuberosus* should be reckoned here or not. Tubers of *Cyclamen* and others certainly do not belong to this class: they are stems.

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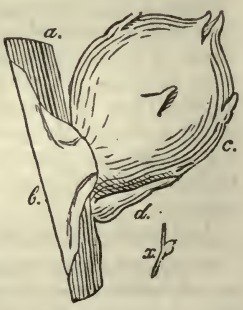


*d.* Tuber buds, tubercles (*tubercula*). Many plants form small tubers above the earth; seldom (if ever?), indeed, as axillary buds, but frequently as adventitious buds, and especially on foliaceous

[177] *Solanum tuberosum.* Bark of a filiform subterranean stem (*a*), cut into at *b* down to the bottom of the axillary bud. *c*, The young potato; *d*, scale-like leaf, which bears the potato as an axillary bud; *x*, outline, of the natural size.

organs, from which new independent plants develope so soon as they are separated from the parent plants: sometimes this is a specific peculiarity; as, for instance, the tubers of the species of *Amorphophallus* and other *Araceæ:* sometimes they arise in certain plants particularly readily in consequence of injuries; as, for instance, in the *Gesneriaceæ* on the broken surface, after cutting a leaf nerve at the edge or the point of the leaf.

These tubercles hold the same relation to the tubers that the bulbels do to bulbs, at least so it appears from what has been already made known upon the subject; for again, all of the plants belonging here are far too insufficiently known in their development to admit of our defining the relations of the tubercles to the occasionally equally tuberculated stem.

*e.* Pseudo-tubers (*tuberidia*). In some plants a single, frequently an axillary, bud is transformed in a peculiar manner. The parenchyma of the axis of the bud, which is situated over the vascular surface, suddenly becomes exceedingly expanded in a solid and tuberculated form, by means of the sudden commencement of new formation of cells in isolated groups of cells; in the axillary bud this only occurs on one side (as in our native *Orchideæ*), since, on the other side, the pressure of the stem prevents such distension. In *Aponogeton distachyon,* the thick fleshy cotyledon with the end of the root proves a corresponding obstruction; hence here, also, the development of the pseudo-tuber is only one-sided. In the Dahlias, on the contrary, the tubercular development is equal on both sides. The mass of cells enters between the base of the cotyledon and the new adventitious roots, arising, at a very early period, almost immediately under the cotyledon, and which, through the formation of the pseudo-tubers, become gradually removed far away from the cotyledon.

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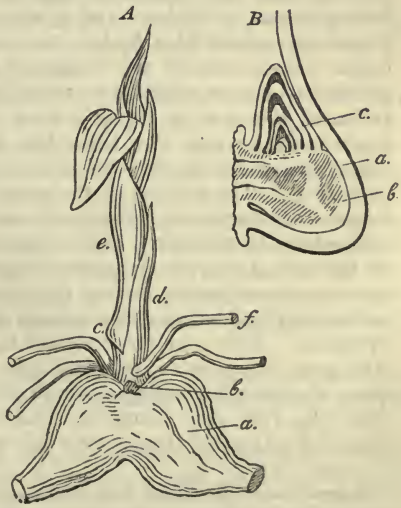


The process of formation of the pseudo-tubers in the indigenous *Orchidaceæ*, especially *Orchis, Anacamptis, Gymnadenia, Platanthera,* and *Ophrys,* which I have investigated in regard to this point, so far as the species were at my command, is in the highest degree interesting; I sketch it here, after examples easily to be verified in *Orchis Morio* (fig. 178.) and *latifolia.* In the axils of the lower leaves (*A, d,*) occur axillary

[178] *Orchis Morio. A,* Natural size, young plant: *a,* tuber of the current year; *b,* scar of that of the former year, cut away; *c,* papilla which indicates the formation of the

buds (*A*, *c*, *b*). Soon after vegetation has commenced in spring the bud of the *second* leaf begins to develop, the portion immediately above its point of attachment first expanding and pushing its way downward (fig. 178. *B*); in *Morio* in a roundish, in *latifolia* in a very early recognisable, two-lobed form. This expansion soon breaks its way through the base of the leaf, in the axil of which the bud occurs, as well as through the vaginal border of the lowest leaf, and thus it becomes visible externally. The part by which the bud is connected with the stalk does not increase in thickness, but merely elongates, whereby the pseudo-tuber, bearing the bud above upon its summit, becomes continually removed further from the parent plant. Toward the close of summer, the pseudo-tuber which has vegetated in the preceding year has become wholly destroyed; that of the current year adheres to the side of the one newly produced, and still bears the remains of its stalk and leaves: the new pseudo-tuber is at least so far perfected that in the following year it is capable of forming roots for the nutrition of the plant. In consequence of this kind of development of buds, every Orchis plant alters its place annually; and, since the lower leaves have an angle of divergence of about 129°, this occurs in such a way, that in the fourth year it returns pretty nearly to its original situation. These pseudo-tubers are decidedly not roots in a morphological sense, in all probability not in a physiological; but at present we have no facts on which to found a decision on this question. On the other hand, in the beginning of spring, many adventitious roots, which subsequently take upon themselves the nutrition of the plant, are always formed from the stem above the pseudo-tuber, and below the first leaf. I have no accurate researches yet on the mode of cell-formation in all this process. The pseudo-tubers are traversed by vascular bundles, which run in great numbers, mostly in arcs, from the apex to the base, and are surrounded by lax, large meshed, cellular tissue, which in an early condition exhibits upon its walls reticular currents of sap proceeding from a cytoblast; cells from six to eight times larger lie embedded in the above, forming circles round the vascular bundles. In very young pseudo-tubers the homogeneous, colourless, and gelatinous contents of these larger cells is tinged of a violet blue by iodine; as the pseudo-bulb grows older, this colour passes through the colour of red wine to yellow, and at last the gelatinous matter exhibits no reaction to iodine. But during the vegetation of the same in the following year, the gelatinous matter changes again in the reverse way, till at last, in the decaying pseudo-tuber, a condition once more appears when the gelatinous substance is not coloured by iodine. The surface of the gelatinous mass manifests in its perfect stage of development markings of minute retriculations, almost granular, somewhat like the starch in the cells of a boiled potato. In the remainder of the cells a very finely grained starch is gradually formed, which disappears almost totally during the vegetation of the pseudo-tuber, so that at last only isolated granules remain in each cell, adhering to the persistent cytoblast. This peculiar structure in our *Orchidaceæ* is to be paralleled with some tubers in the tropical kinds, in which, in like manner, the formation of a tuber only changes one single internode; for instance, *Bolbophyllum* (fig. 179. *A*), *Gongora*, *Rodriguezia*, *Epidendrum* (fig. 179. *B*). But in the tropical *Orchidaceæ* this structure passes through forms such

next year's tuber; *d*, lowest leaf of the plant; *e*, second leaf, in the axil of which the plant and tuber of the next year are formed; *f*, adventitious roots cut off. *B*, Longitudinal section through *c* of the preceding figure: *a*, lower part of the leaf; *b*, rudiment of the tuber which is formed out of the base of the axillary bud; *c*, axillary bud, the rudiment of the next year's plant.

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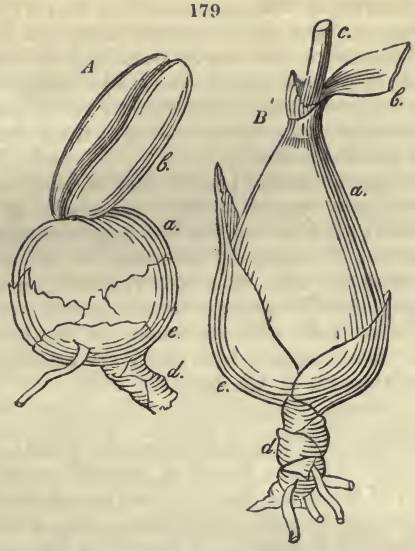


as occur in *Bletia* into the true tuber, through *Monachanthus*, *Catasetum*, *Dendrobium*, &c., into the usual structure of stems. In an exactly similar manner to that in *Orchis* is formed the pseudo-tuber of *Aponogeton distachyon*. The embryonary bud is attached laterally and free upon the thick, fleshy cotyledon; the *radicula* is developed quite regularly at first, in germination; but the portion of the embryonary bud between the cotyledonary leaf and the following soon swells up into a fleshy body on the free side, and then the full-grown, round pseudo-tuber becomes separated from the cotyledon, while adventitious roots have been gradually developed between the pseudo-tuber and the lowest leaf of the young plant.* I do not know whether new pseudo-tubers can develope in *Aponogeton* as axillary buds of the plant.

Lastly, in reference to the Dahlias, my investigations are still very imperfect. The matter appears to me to stand thus: Two adventitious roots are formed on the base of the cotyledon soon after germination. In later conditions I found the young pseudo-tuber (no trace of adventitious roots) under the cotyledon, but two of them pretty low down upon the pseudo-tuber: I think these must have been developed between the former adventitious roots and the cotyledon. I have given at length, in my already often-quoted treatise on the *Cacteæ*, an account of the process of multiplication of cells in the young tubers, contemporaneously with the origination of oil passages. It consists in constant formation of cells

* What Planchon (Ann. des Sc. Nat. 1844, Botanique, p. 107, et seq.) has published on this is altogether incorrect, and, like a good deal else in the same essay, a result of very superficial observation.

[179] *A*, *Bolbophyllum bulbiferum*, natural size: *a a*, tubercular internode, the terminal bud of which becomes the inflorescence; *b*, leaf; *c*, dry, old sheathing leaves; an adventitious root is breaking forth through the lowest; *d*, older and non-tubercular internode. *B*, *Epidendrum cochleatum*, two-thirds of the natural size: *a*, *b*, *c*, *d*, as before; *e*, the flower-stalk, cut off.

within cells and absorption of the parent-cells. In very young tubers this process of development goes on in a zone outside the vascular bundles; at a later period it enters into many situations throughout the whole tuber—in vertical rays in the pith, in horizontal ones in the rind. In all the young pseudo-tubers all the cells exhibit most beautifully a circulation branching out in reticulated currents from the cytoblasts, and running with the greatest rapidity.

All these forms here sketched have this in common, that they are tubercular thickenings of a portion of an internode, at most of a whole one (in the Dahlia), this alteration not contemporaneously affecting the foliaceous organs or buds; by this they all fall within a common definition, and are at the same time clearly distinguished from the true tubers, which always comprehend an entire axillary bud, *i. e.*, all the internodes of an entire axis with its foliaceous organs and buds. The so-called bulbs of Crocus belong here: they are nothing but the fleshily-thickened bases of the axis of the bud.

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In the great abundance of so-called tubercular plants, it is very possible that other and quite different forms of peculiar modifications of buds occur; on account of the great dearth of our knowledge of their development nothing more can be said about them — nay, the examples of the forms noticed cannot be increased. A time must first come when the now usually so dry and spiritless systematic works will give something more than *Planta tuberibus perennans* or *Radix tuberosa*, &c. Such investigations are in the power of every one who has a tolerably good simple microscope, which may be bought for a very little money; and they would further science more than the description of one hundred new species in the superficial way just adverted to, from which one in fact learns nothing more than that they exist upon the earth.

Seed-buds (ovules, *gemmulæ*). The last terminal and axillary buds in the interior of the blossom assume a wholly peculiar form, of which, however, I cannot speak until I come to the examination of the apparatus for propagation.

## E. THE FLOWERS.

§ 137. We include both: *a*, every single organ of propagation by itself, wherever unconnected with others on the same axis, through a *circle* (or compressed spiral) of modified foliar organs (floral envelopes), and *b*, every combination of several organs of propagation, collected within *one* floral envelope, and separated by this from others, — under the name of flower (*flos*); on the other hand every collection of single flowers is an inflorescence (*inflorescentia*).

If we review the whole kingdom of Phanerogamous plants, and seek in the multiplicity of forms for a guiding clue, our impressions will lead us to something like the following ideas:—

Two *morphologically* fundamental organs, axis and leaf, modified toward this object in the preceding groups of plants; and two *physiologically* determinate organs, serving for reproduction, propagative cell, and seed-bud (*ovule*), gradually developed; the formative force of nature now connects the propagative cell (*pollen*) with the leaf (*anther*), and the seed-bud with the axis. We thus obtain two organs of reproduction at

once morphologically and physiologically determinate, two sexes (*sexus*). But these have no definite relation to each other *in space;* this or that leaf may be transformed into a stamen, this or that axis into a seed-bud, on any individual plant. It is not inconceivable that we may yet discover a plant in which, without any apparent arrangement, here sometimes only a stamen, there sometimes only a common terminal bud, is developed into a seed-bud. But Nature seeks gradually to unite the two parts continually closer, and thus we obtain, on a general survey, the following stages of development in the *Phanerogamia.*

1. Isolated stamens and seed-buds, at first in different individuals, then united in one individual, constituting in their forms the gradual transition from the *Cryptogamia* to the *Phanerogamia*, become finally united in great numbers upon *one* axis. With exception of the very simplest, yet to be discovered case, we have this in the *Cycadaceæ*, *Coniferæ*, and *Loranthaceæ.*

2. Inflorescences of this kind, in the simplest form, become surrounded by a foliar organ of a peculiar form (*spathe*), and at the same time the seed-buds become enclosed in a peculiar case (the germen in *Lemnaceæ*). Gradually, at first through the position, then through the addition of bracts (?) groups of stamens become collected around the germen (*Araceæ*, *Naiadacæ*, *Orontiaceæ*).

3. A circle of definitely modified foliar organs, encloses as floral envelopes, the stamens or germens into monosexual flowers (*Hydrocharideæ*), or finally both into hermaphrodite flowers (*Liliaceæ*).

4. Now succeeds the development of the complete flower into the greatest multiplicity of combinations of the different parts and their forms, in a great number of Mono- and Di- cotyledonous families.

5. The single flowers approach closer together in the manifold forms of the infloresence, in many other families.

6. Finally, the entire inflorescences contract so closely, and into such a limited form, that they again appear like one simple whole; the so-called compound flowers, the highest stage of development of Phanerogamic structure, on one side rising according to the Monocotyledonous type through the Palms to the Grasses, on the other, according to the Dicotyledonous type, preceded by the inflorescence partly of the *Umbelliferæ*, partly of the *Leguminosæ*, to the *Compositæ.*

Thus we receive the impression of an incessant gathering of a greater number of individual parts, under continually closer morphological connection, into a unity, and of an unbroken series of gradually increasing complications of fundamental organs, which are naturally divided according to their principal stages, into imperfect flower, flower, inflorescence, and compound flower. But this is merely the æsthetic conception which gives us the idea of Nature working like a human being, according to a certain plan, and continually concentrating this. In the scientific treatment of the matter we require very different and more accurate limitations, of the definitions, in which no transitions, confusing the distinctions, are possible.

It does not seem to me that hitherto much pains have been taken about the accurate perception of the definition of a flower, or that we have been very fortunate in the discovery of the correct expression. According to most definitions yet given, it would be rather difficult to distinguish between flower and inflorescence. Kunth, in his Botany, speaks of the flower, without anywhere saying what this may be, wherein its essential characters consist, and what are the limits of the definition of it. Bischoff does the same, in his Botany.

Link says: "Flower is a bud altered through metamorphosis: it belongs to the terminal parts, and is known by the stamens and pistils." How Link will by this means distinguish the inflorescence of the *Araceæ*, of the *Compositæ*, &c. from a flower, I do not see; both are metamorphosed terminal buds, with stamens and pistils; no investigation can establish that the bud is a compound one in the former, which, indeed, is not set up by Link; for every leaf-bud, for instance, in the Lime, has lateral buds; and the greater or smaller development of lateral buds cannot at all come into consideration in a *metamorphosed* bud.

Lindley calls the flower a terminal bud which encloses the propagating organs, and the foregoing objection is so much the more applicable to his definition.

A. Richard says, "The flower is essentially constituted by the presence of one of the sexual organs, or of both sexual organs united on a common organic receptacle; they may, or may not, be furnished with a definite envelope to protect them." This suits so excellently the cones of the *Coniferæ* and the spadix of true *Aroideæ*, that Richard cannot truly deduce from his definition of the flower why, by his rule, those are inflorescences and these flowers.

These examples are sufficient to make good the reproof, that hitherto Botany has never raised the question how the flower is distinguished from the inflorescence, and yet the answer to this question is indispensable.

The language of common life, starting from the unprejudiced impression, calls the spadix, with its spathe, the flower of the *Araceæ:* it speaks of the flower of the Clover, and means the entire head; it says the Cornflower, and applies this name to the whole *capitulum* of *Centauria*. The simple impression is at first always right; and if science, in opposition to it, calls those flowers not flowers but inflorescences, it must prove this against the simple impression. This may, of course, be done satisfactorily, but has hitherto been altogether neglected. Link* even sought to defend the popular term in the *Compositæ*, against Cassini; when he says, however, that the people appear to have had a better *knowledge* of the *essential* of the inflorescence of the *Compositæ* than Cassini, it is indeed merely a jest. The people call the thing a flower for the very reason that they have *no knowledge at all* of what is *essential* in the matter, but refer merely to the impression of first sight. An obscure presentiment of something true does, indeed, lie in this unprejudiced perception, as in the natural piety of the clown is indicated, even though in obscure features, the Divine faith resting deep in the human spirit; but he who would endeavour to develope a philosophy of religion with the limited insight and confused conceptions of a clown, would arrive merely at confined and obscure mysticism. Science, in order to gain a distinct consciousness of that which lies dark and hidden in impression and feeling, requires scientific instruments, accurate abstractions, definite conceptions, &c. Undoubtedly there lies in that complication of single flowers into that which gives us the impression of *a whole*, with definite limitation in the *Compositæ*, &c, something which marks it as a higher morphological stage of development of Phanerogamic plants; and it is just this new combination of isolated parts into a collective form of a higher order which the unprejudiced popular sense at once comprehends. But these forms do not thereby stand nearer to the solitary flower than to the inflorescence, as Link supposes†, but are, on the con-

* Elem. Phil. Bot. ed. 2. vol. ii. p. 78.

† This would be the same as saying 1000 stands nearer to 1 than to 999.

trary, separated from that by the entire series of different inflorescences, and are gradually prefigured through these until they form, themselves, a thoroughly new and more elevated unity. Of *this* unity of an entire inflorescence we not only have, as yet, no scientific characterisation, but it is even impossible at present, because we do not know sufficient of the morphological laws of the plant in general, on which that unity also depends. One thing, however, I am firmly convinced of; namely, that we have, as De Candolle has already half done, to regard the *Compositæ* as the completion of the morphological development of the Dicotyledonous plant, and the Grasses, which Link very sensibly places by the side of these, as the highest stage of the Monocotyledons. In this view, also, have I described the higher gradations of the *Phanerogamia* as continuations, as it were, of those previously given.

But this way of looking at the matter, as I have already said, has, at present, merely an æsthetic value, and such mingling of æsthetics with science inevitably turns the latter from its purpose, and paralyses its progress; therefore I must oppose to this survey the rigid scientific definition of the paragraph. We cannot enter at all upon that mode of development, because its stages are not distinct divisions; they rather rise *gradually* from one to another, and thus cannot be kept apart with strict scientific accuracy. In the examination of the heads of the *Umbelliferæ*, the *Leguminosæ*, &c., especially, the distinction between inflorescence and compound flower so completely confuses us, that it appears totally impossible to obtain a definition which will strictly distinguish them. On the other hand, the explanation of flower and inflorescence, above given, furnishes us with quite strict distinctions, by means of which we may readily comprehend each other in all scientific doings; but this comprehension is useful solely in scientific terminology. If now, after this discussion, we consider some of the doubtful phenomena, we very readily come to a decision whether we shall call any thing a flower or an inflorescence. In the first place, I will present the case of the male flowers of the *Coniferæ*. In *Abies* we find a bud, of which the lower leaves are developed, as in every leaf-bud, while the upper are converted at once into stamens*; here we have the simplest flowers connected with the simplest inflorescence, not, however, forming altogether a solitary flower: the only analogue is the inflorescence of the female flower.† Here is a bud the leaves of which cannot bear seed-buds, from the very fact that they are leaves; but in every axil of such a leaf (bract) an axis‡ arises, and produces two seed-buds. In all the *Cupressineæ* the formation of the male inflorescence is the same; in the female the seed-buds appear to be axillary buds (with adventitious buds) of the bracts.

According to the definitions given the proof is further afforded at once, that the spadix of the *Araceæ* is to be explained as an inflorescence, because it has no bract (and even in the simplest case, where only one germen, with one stamen, on a spadix developed merely as a little node, are enclosed in a scarcely visible membranous spathe, as in *Wolffia*).

* That the anther is here adherent to the back of a bract is another of the purely ideal fictions; as if there were not hundreds of *antheræ extrorsæ*, or of *antheræ cristatæ*

† In *Abies alba* it not unfrequently happens that a portion of the lower leaves of the female inflorescence become converted directly into stamens; but then no axillary buds are developed.

‡ In *Juniperus* I guess, from yet imperfect researches, that the conditions are wholly identical, and only vary by the seed-bud standing upright, instead of being suspended, as in *Abies*.

Lastly, I will just offer a few remarks on the enigmatical family of *Podostemaceæ*, in which we cannot yet well decide whether the complication of germens and stamens together is to be accounted a flower or an inflorescence. The history of development is altogether unknown; young buds of *Podostemon ceratophyllum*, preserved in spirits exhibited to me the two stamens so closely approximated to the germen on the scarcely perceptible stem, that the bract (?) standing on its base almost formed a regular ternary circle with the two situated on the germen; it may be that the parts of a solitary flower are here thus separated by eccentric development, since, in some others, e. g. *Tristicha* Thou. (*Dufourea* Willd.), a regular ternary floral envelope encloses a germen and a stamen, and the flower appears tolerably regular in almost all the remaining genera.

§ 138. The following points must be taken into account in the flower, deserving a more minute discussion, and they will, therefore, constitute the next sections: 1. The arrangement of the flowers upon the plant, inflorescence, and the foliar organs standing in relation thereto, the bracts and bracteoles; 2. The parts of the flower at the epoch of blooming; 3. The transformation and development of the parts of the flower into fruit; 4. The parts of the flower at the time when the seed is ripe.

Many matters I shall relate briefly, because they have been treated previously in the proper places, and may conveniently be left out here. I had rather, however, be useful in indicating a necessary reform of science, than bring confusion and injury upon it by an ill-timed radical revolution.

## I. *The Inflorescence.*

§ 139. It has already been stated that the inflorescence is nothing else than the axis and its ramification where all the buds are flower-buds. We here distinguish the solitary flower, either as a terminal flower (*flos terminalis*), or as an axillary or lateral flower (*flos axillaris*). The latter is sometimes naked (*nudus*), on account of the suppression of the *folia floralia*, or *bracteæ*. If the lateral branch bears only one flower and bracteoles besides, it is called a pedicel (*pedicellus*) below the flower, and the axis, to which the pedicel is an axillary shoot, is called the peduncle (*pedunculus*). The assumption of a pedicel to the terminal flower is purely arbitrary, and at most to be maintained only by the presence of bracteoles, and an articulation of the axis. The accumulated flowers always stand, in a rudimentary condition, in a *capitulum*. From this, by extension of the flower-stalk (*pedunculus*, here called *rachis*), comes a spike (*spica*), by development of the pedicels an umbel (*umbella*); by development of both, a raceme (*racemus*): these are called the simple forms of inflorescence, and in reality there are, and can be, no others. If an inflorescence be enclosed in a single large bract, this is called a spathe (*spatha*); if, on the contrary, it be enclosed in a circle or contracted spiral of bracts, the envelope formed by this circle of bracts is called the involucre (*involucrum*). The simple inflorescences may become combined in manifold ways, on which a number of useless terms have been founded, with reference to the

course of development, and composition, mostly merely naming the peculiar mode of appearance in particular families; e. g. *anthela* of the *Juncaceæ, glomerulus* of the *Cyperaceæ;* according to others, also, of the *Amarantaceæ* and *Chenopodiaceæ*, moreover *panicula, fasciculus, thyrsus, cyma,* &c. with altogether indeterminate definitions.

If the manufacture of words, without principles of definition, without thorough investigation of particulars, has prevailed anywhere, it has in the study of the inflorescence. The study of the fruit perhaps excepted, there is no part of Botany in which prevail such confusion, such a wild waste of synonymes, and yet such imperfection and incompleteness of the whole subject, as here. Perhaps Linnæus even shares the blame here; for certainly no part was so superficially treated by him as the inflorescence which he named, without starting, as elsewhere, from accurate definitions, merely according the superficial impression of some few conditions with some words not even defined, but explained by examples. In this path others followed, and only Röper, opening a new way, furthered the study in many respects, yet without finding or ensuring accurate results. As yet we have not the history of development of one single inflorescence, though many fancies indeed, as they have originated one out of another. Since no principles can be laid down for such play of imagination, every one has his own, and every one takes the matter in a different way, not merely in the more complicated, but, in some measure, in the simpler forms of inflorescence. What a quantity of paper has been written over during the last fifty years, on the import of the extra-axillary inflorescence of the species of *Solanum*, on the spirally coiled inflorescence of the *Boraginaceæ !* but has one single botanist made an attempt to look how they are formed, in order thus to explain their nature? And, disregarding this, what illogical confusion is exhibited in the common classification of inflorescences by almost all authors! The inflorescence, say most, is the arrangement of the flowers upon the stalk. The division, therefore, can only be founded on the difference of arrangement. But very few inflorescences are defined according to this; the spadix is distinguished by the substantiality of the rachis; the catkin, by the articulation with the plant, or with Bischoff by the nature of the flowers; the *corymbus* and *fasciculus, panicula* and *cymus,* according to Lindley, by the order of blossoming. Link, on account of the imaginary want of bracts in the *Ficus*, makes a new word, in opposition to the *calathium* of *Compositæ;* but he calls the bractless raceme of the *Cruciferæ* a raceme. Forms of inflorescence are distinguished by the order of opening of the flowers; but the inflorescence of *Dipsacus*, which opens its flower from the middle upward and downward, is a *capitulum*, like those which open the flowers from below upward. Here it is absolutely impossible for one individual to devise means; only the earnest co-operation of many, especially of those who have authority in science, will be sufficient to introduce gradually a better and simpler, consequently an easier, treatment of the subject. But when will the time come wherein the majority of botanists will, not seemingly, but according to the spirit and the truth, keep science steadily in view, instead of themselves and the gratification of their own vanity?

Starting from the simplest case, we gain the following mode of viewing the subject. Flowers originate from buds, and these originate, except the terminal bud, normally only from the axils of leaves. The first and simplest inflorescence is, consequently, the solitary flower at the

end of the axis, or in the axils of its leaves. In the terminal flower the axes of the flower and of the stem are identical; therefore a pedicel is only to be distinguished when true articulation warrants a division of the axis, or the true leaves suddenly pass into bracteoles. In a gradual transition no distinction is possible. The leaf, where the axillary bud becomes a flower, is called a floral leaf; if it deviates importantly in form and substance from the common leaves of its plant, it is called a bract. But this transition from floral leaf into bract is not sudden, as both, in a rudimentary condition, are exactly similar foliar organs, so we often find on one and the same stalk all intermediate forms between them; and, for instance, in *Veronica fruticulosa*, *Delphinium Ajacis*, *Epilobium angustifolium*, *Verbascum thapsus*, &c., no one can declare where the floral leaves cease and the bracts commence: thus the distinction between many solitary axillary flowers and a spike or raceme becomes already a very uncertain one, which in the perfect plant cannot, indeed, be strictly sustained in the examples referred to. But the deviation from the common leaf often goes still further: the leaflets (bracts), distinct and green in a rudimentary condition, e. g. in the Dahlias, become little dry shreds of membrane in their perfect development, and are called *paleæ**; or they are altogether stunted, so that no trace of them can be perceived in the perfect inflorescence (as in the *Compositæ* to which is ascribed a *receptaculum nudum*). In like manner we find a stunting and final disappearance of the bracts in the *Umbelliferæ* and *Boraginaceæ*. Among the former, in which the entire complication of bracts in the simple umbel is usually called an *involucel**, in the compound one *involucre*†, *Scandix Pecten*, *Astrantia caucasica*, *Bupleurum*, and *Eryngium* have true floral leaves, which pass gradually into bracts, such as alone exist in *Daucus hispidus* and *Hasselquistia cordata*, *Oreomyrrhis eriopoda*. In *Petroselinum sativum* and *Heracleum speciosum* the bracts of the compound umbel are already stunted; in *Caucalis pulcherrima*, wholly gone: in *Chærophyllum aromaticum*, also, the bracts of the simple umbel are small; in *Anthriscus*, quite stunted internally: finally, in *Pastinaca*, *Anethum*, and *Pimpinella*, almost all have disappeared. In the *Boraginaceæ* the floral leaves pass gradually into bracts in *Cerinthe*, in *Lycopsis* the bracts are arrested in development upwards, finally, absent in *Symphytum*.

The *Cupuliferæ* exhibit another peculiarity: one or more circles of bracts (e. g. in *Fagus*), or bracteoles (e. g. in *Quercus*), become blended with each other, and continue to grow with the ripening fruit. This has been called a *cupula*.‡ Something similar occurs in the bracts of *Euphorbiaceæ*, where ten bracts are usually blended together, the free apices of the five inner being usually different and bent inwards, while in the outer the perfectly free apices, or the bases of them, become developed in a fleshy (glandular) manner. Both phenomena fall completely within the definition of the spathe. In the *Cruciferæ* there appear to be scarcely any exceptions to the rule that no bracts exist; and yet I believe I may

* Altogether superfluous terms.

† Better partial and general involucre.

‡ Link (Elem. Phil. Bot. ed. 2. vol. ii. p. 109.) says the cupula does not yet exist in the flower. He has apparently never looked into a flowering Cupuliferous plant. Moreover, there is not here any peculiar part with leaves grown to it, as he says, but the cupula originates *solely* from blended leaves. The cupula has no similarity to the succulent coat of the seed of *Taxus*, and is not, as Link says, proper to the *Amentaceæ*, since, in the true *Amentaceæ*, it does not occur at all; only in the *Cupuliferæ*, which hence derive their name.

venture to assume, from some investigations (but few, I own), that they do exist everywhere in rudiment, as, for instance, in *Iberis*.

As, on the one hand, very crowded inflorescences become stunted, especially in the internal part, so in the excessive development of bracts, the flowers in their axils are frequently abortive, chiefly in the outer parts of a very crowded inflorescence (sterile bract, *bractea sterilis*). To this are referable the common calyx (*calyx communis, anthodium*, &c.) of the *Compositæ*, the similar circle of leaves which close the mouth of the Fig, the outer scales of the Grasses (*gluma* Juss., *calyx* Linn., *lepicena* Rich., *tegmen* Palisot, *glumæ valvæ* Link), which either both or one, sometimes the upper—sometimes the lower—have no flower in the axil. Link acutely remarks on this point, that the Grasses have a compound flower in respect of this, or more correctly an inflorescence, similar to that of the *Compositæ*. We may apply to all these combinations of bracts the general term blossom-envelope (Bluthenhülle), which will then comprehend the *involucrum* of the *Umbelliferæ*, the *calyx communis* of the *Compositæ*, the *cupula* of the *Cupuliferæ*, the *involucrum* of the *Euphorbiaceæ*, the *gluma* of the Grasses, &c.; and, by joining a clearer and more accurate distinctive name to the definition, at once free us from a vast waste of terminology.

From these considerations the general law may be expressed, that, excepting as a terminal flower, the solitary flower always, and only, appears in the axil of a leaf, or in the place corresponding to that axil.

As in the branch-buds the distinction was required between principal and secondary bud, so also here; of which condition I believe no one has hitherto thought: yet such secondary buds distinctly exist, for instance, in the inflorescence of *Apocynum androsæmifolium, hypericifolium*, &c. It is very difficult to say whether the peculiar condition of the inflorescence, e. g. in *Penstemon*, belongs here, where, instead of one (terminal) flower in the bifurcating division of the peduncle, there are two, of which one with a longer pedicel projects beyond the other. In like manner, the position of the flower of *Helianthemum variabile* seems to me to be diverted toward one side of the pedicel, because it originates from a secondary bud, while the terminal bud does not become developed.

Another peculiar condition exists in the bract of the Limes. The axillary bud, formed every year to persist through the winter, has two opposite lateral bud-scales quite to the outer side, one of which remains in this condition. But a bud is formed in the axil of the other, developing the same year, and becoming blended with the bud-scale, which grows up with it, forms the peduncle, and thus exhibits a very decided example of *prolepsis*, which outstrips the *homologous* organic parts of the plant at least by three years. An actual blending of the pedicel with the bracts, like this, occurs also in the male flowers of many *Cupuliferæ*, e. g. in *Corylus*, and in the flowers of *Saururus*.

Finally, it must be noticed, that it very often happens, especially in the peduncle, that the substance expands to a greater extent in the points which are not the bases of the parts seated on it, and swells up around those bases. Thus the parts attached upon it appear to have their base sunk in little pits (e. g. in the *receptaculum foveolatum* of the *Compositæ*), or completely imbedded in little cavities in the uniform mass, as in the female flowers of *Dorstenia*. This condition occurs naturally most frequently on very thick peduncles, developed into a woody or fleshy substance.

A number of flowers, again, may be so collected together that they appear more closely grouped, and assume a collective form. We must first look at the simplest case as the basis, and this is afforded by the progressive development. In a bud are formed internodes, which are parts of *one* axis (here called *rachis*, or better *peduncle*, whereby *one* useless word will be got rid of), together with the leaves belonging to them, and in the axil of every leaf a bud which develops into a simple flower. In the rudimentary condition the internodes are undeveloped, but this development is something coming into action at a subsequent period; consequently, the inflorescence which is simplest and nearest to the solitary flower, is the *capitulum*, an axis composed of undeveloped internodes, with an axillary (flower) bud, the first internode of which is not elongated. From this basis are developed all other simple forms of inflorescence. The slightest possible alteration is the development of the internodes of the peduncle. If this happen in the longitudinal direction, the inflorescence is a spike (*flores in pedunculo elongato*); if horizontally, a *calathium* (*flores in pedunculo disciformi*); if the expansion take the form of a cup, it is a Fig (*flores in pedunculo concavo*)* ; lastly, if the peduncle elongate and become at the same time very fleshy, it is a club, *spadix* (*flores in pedunculo elongato carnoso*). But these forms do not constitute distinct members of a series: they pass almost insensibly one into the other; even the distinction between *capitulum* and *calathium* is not capable of being maintained, and those between spike, *spadix*, and *capitulum* (e. g. the *capitulum elongatum*) are just as uncertain.

The second are the internodes of each single flower, which may be developed in the same way; attention has hitherto been paid only to the one condition of development in length†, in the first internode between the axis and floral parts (the pedicel‡). By this a *capitulum* becomes an umbel; a spike, a raceme. The raceme and spike may then be again more closely defined, according as the flowers stand spirally (e. g. *spica spiralis* in *Gymnadenia odoratissima*); in whorls (e. g. *spica verticillata*, in *Myriophyllum verticillatum*); pinnate or two-ranked (?); one-ranked (e. g. *racemus monostichus* in *Myosotis palustris*); or lastly, all turned in one direction (e. g. *racemus secundus* in *Digitalis purpurea*), &c.

The pedicel is an internode of the floral axis, and in fact the one or *more* occurring between the axil of the leaf of the axis, on which the flower is situated, and the first foliar organs of the flower, or the last internode between the last leaf or bracteole and the terminal flower-bud. This internode may remain undeveloped just like a branch-bud (*flos sessilis*), or become more or less elongated, or even acquire a fleshy con-

* This only differs in a *relative* manner from the *calathium*. Link (El. Ph. Bot. ed. 2. vol. ii. p. 75.) gives as the distinction, that in the Fig the *calyx communis* is wanting, whence it would appear that he has never examined one; and when he says that it originates from blended inferior calyces (that is, inferior ovaries), the words have no sense; since *Ficus*, like all its allies, has *perfectly* superior ovaries, and the flower is even stalked inside the Fig. Nothing whatever is blended here. The cup-shaped peduncle in the Fig is simple from its origin, and is so for a long time before any trace of a flower can be seen. When the flowers are in the condition of buds, it is still smooth, and only closely covered by the *involucrum*, as in the *Compositæ*.

† Whether any other occurs at the time of flowering I do not know.

‡ Another proof of the want of logical acuteness which one meets with in all manuals. It is the gravest error in scientific terminology to have two words for one thing (*pedunculus* and *pedicellus* for the internode beneath a flower), and then to apply one of these words to a widely different object (*pedunculus* to the axis on which flowers are situated).

sistence at a later period, e. g. *Anacardium*, &c. It differs still less from the lowest internode of an axillary twig * than the flower-bud does from the leaf-bud. Both are developed sometimes before the unfolding of the bud (e. g. in the so-called *gemmæ stipitatæ* in *Liriodendron*, and the flower-buds in *Asclepias*), sometimes during its unfolding (e. g. leaf-buds in *Tilia*), sometimes not at all (e. g. lateral branch of *Ligustrum vulgare* and every *flos sessilis*).

The simple forms of inflorescence just mentioned, may combine again in manifold ways into compound inflorescences. We have here to distinguish the homomorphous (pure) from the heteromorphous (mixed), e. g. the so-called *spica* of the Grasses is a *spica composita;* the *umbella* of the *Umbelliferæ* an *umbella composita* = pure inflorescences. But here we must necessarily distinguish between a capitulum and an umbel, originating from the combination of several, and yet similar to a simple inflorescence, both from the actually simple and the *properly* compound (*capitulis capitatis, umbellis umbellatis*). I would propose for this the name polycentric, since in capitula and umbels the undeveloped axis represents, as it were, a centre from which the flowers go out. Such polycentric capitula and umbels occur in most *Labiatæ*, e. g. in *Marrubium infloresc., capitula polycentrica spicata.* The panicles of most of the species of *Bromus* and *Festuca* are *spicæ umbellatæ umbellis spicatis*, or *spicæ racemosæ racemis umbellatis, umbellis spicatis.* The *anthuri* of *Rumex* are (polycentric?) *umbellæ* (*capitula*) *spicatæ spicis racemosis;* the inflorescence of many *Labiatæ, umbellæ* (or *capitula*) *spicatæ* = heteromorphous inflorescences, &c. But here the mistake of the present mode of treating the inflorescence comes in, that definite forms of inflorescence are predicated fully of particular families, and thus combinations of the most varied nature included under one name. Under panicle are comprehended the most heterogeneous inflorescences possible, and the definition can only be such as "All inflorescences of the Grasses which are *not spica composita* (*spica*)," therefore a definition logically incorrect. So in many systematic works every inflorescence among the *Junceæ* is called an *anthela;* but how is it possible to distinguish this multiplicity of inflorescences by one name, if we hold views at all sound of scientific terminology? Is it not the most frivolous trifling with words to name umbels, capitula, spikes, racemes, and all their combinations, *anthela,* and yet to distinguish *anthela, capituliformis, spicæformis*, &c., when *anthela* cannot here mean anything but *inflorescentia Juncearum?* It is inconceivable that a man scientifically educated (not merely taught) can seek and find science in such ringing changes on words. And this not all: the term *anthela,* although it has no meaning, must also be applied to the inflorescence of the *Cyperaceæ*, which, with its stunted flowers combined into a spike, is entirely different in its essential nature. The cause, indeed, lies in this: — It is found too troublesome, in the cases of very complicated

* Link says it grows forth after and beneath the flower, and is thus distinguished from the twigs. If he had actually traced the development of a few flower-buds, he would know that there is nothing in this. Every branch-bud is formed, like the flower-bud, as a *gemma sessilis;* whether it developes single internodes longitudinally afterwards is a matter which varies equally in both. Link says further, that it wholly or partially withers with the flower (he should have said with the fruit or male flower), and, indeed, falls off; a peculiarity which it shares with all annual stems (e. g. with *Aquilegia, Aconitum,* umbelliferous plants, &c.), which therefore does not distinguish it.

inflorescences in particular families, to investigate minutely their composition from simple inflorescences; and it is found more pleasant to make a collective word, which may then be defined a little closer (although very superficially) by a few adjectives. To this want of profundity we owe the catalogue of sins of synonymy*; since in the total want of scientific ground for such modes of naming, every one has an equal right to assert his imaginary wisdom.

§ 140. Both peduncle and pedicel may fall off soon after the development of the flower (*p. caducus*), e. g. the male flowers of *Salix*, &c., or with the ripe fruit (*p. deciduus*), e. g. in *Cerasus avium;* or remain upon the axis after the ripening of the fruit and scattering of the seed (*p. persistens*), e. g. *Aquilegia vulgaris;* or even become altered in various ways by growth, during the ripening of the fruit (*p. excrescens*), e. g. *Anacardium, Hovenia dulcis*, &c.

That each part of a plant may endure for a shorter or longer period, may remain in connection with the entire structure for a shorter or longer time, and undergo alteration in various ways subsequently to its first appearance, is not peculiar to the peduncle and pedicel; and, instead of saying this once and for all, it is superfluously repeated for every part in botanical manuals, as though there were a lack of matter. In the study of the inflorescence, however, a special import has been attached to this universal property, and the spica and amentum have been distinguished according to it. The three first conditions do not belong at all to morphology, but are vital phenomena; the last is referable to the morphology of the axial organs, not of the inflorescence. But I was obliged to mention the matter here to prevent obscurity in the following review of the kinds of inflorescence usually admitted.

§ 141. It is dependent on some peculiarities connected with the vitality of the plant, the causes of which are unfortunately still quite unknown to us, and can only be perceived as special properties, that sometimes this, sometimes that, portion of the whole plant, but in a specifically regular course, is advanced in growth and development toward perfection. This is seen in the flower-buds, which open and blow in regular procession, according to definite laws. On the simple axis only, the following conditions occur:—

1. The unfolding of the flowers follows the order of their age. The older flowers, lying undermost, bloom first; and the upper ones gradually follow. This is termed a centripetal inflorescence (*inflorescentia centripeta*). It occurs in *Philadelphus, Isotoma axillaris.*

2. The unfolding of the flowers follows the reverse order, so that the upper and latest-formed buds open first, and the older ones follow in regular course. This is termed a centrifugal inflorescence (*infl. centrifuga*); it occurs in *Clematis integrifolia, Saxifraga*, &c.

* The vanity of wishing to be referred to is the parent of most useless words; and this disease will not come to an end until the catalogue of synonymes is understood to be a botanical pillory, wherein a man becomes abased lower for every time he stands in it: then people will be careful of making new words, without sufficient scientific grounds. Of such men as Robert Brown I am not afraid; for those people always make the most new words who are least capable of doing actual work in science.

3. The blooming follows no such simple order; it may commence in the centre, and proceed both upwards and downwards simultaneously, as in the capitula of *Dipsacus;* or the upper and middle buds may begin to open simultaneously, and the blooming proceed downward in two divisions, as in *Campanula Medium.* This may be termed indefinite inflorescence (*infl. vaga*).

In compound axes the same condition occurs with respect to main axes and adventitious axes, and is by no means necessarily uniform with the law for the simple axis. Thus, in most *Compositæ* the *infl. centripeta* frequently occurs in the single capitula; and *infl. centrifuga* in the side branches, in relation to one another, as occurs in *Centaurea calocephala:* in *Sanguisorba,* on the contrary, the main capitula, as well as the side branches, exhibit *infl. centrifuga.* The generality of the *Labiatæ* exhibit in the inflorescence of the individual side branches, an *infl. centrifuga,* whilst the branches themselves are centripetally developed.

This relation of condition, as is self-evident, is one altogether foreign to the inflorescence, i.e. the *arrangement* of the flowers, and belongs to the vital phenomena of the plant as a whole; unfortunately, however, through want of clear logic, it has become entangled in the study of the inflorescence, and I was therefore obliged to refer to it here. Any brain with a little logic in it, will readily see that the course of the unfolding of the flowers does not possess *equal* importance with the arrangement of the single flowers, in establishing the various kinds of inflorescence; but at most may subordinately contribute, in *one and the same species* of inflorescence, specific distinctions for single groups, genera, or species of plants.

§ 142. Upon the condition of structure we have here little to say, since this subject was necessarily forestalled in the axis and leaf; and here only relations of position alone come into the question. The bracts and bracteoles are commonly formed of thin-walled cellular tissue, delicate, and often coloured*; sometimes in entire families of plants, they are perfectly dry and sapless. The vascular bundles of the pedicels sometimes stand in definite proportion to the number of the floral leaves.

### REVIEW OF THE INFLORESCENCE IN GENERAL.

§ 143. *A.* The solitary flower, as terminal or axillary flower (*flos solitarius, term. vel axill*). The latter may be situated in whorls, and then form a verticil (*verticillus*).

### B. *Simple Inflorescence.*

#### *a. Inflorescentia centripeta.*

1. The *capitulum.* The undeveloped axis is here usually enlarged upward, with a fleshy or spongy substance, and the more

* *Coloratus,* i. e. of some other colour than green.

so if the number of flowers is very great. It may be more minutely designated as simple, discoid, cupulate, lageniform, conical, and cylindrical, as it approaches nearer to one or another. The last form then passes gradually into the spadix.

Special varieties are: —

*a.* The *calathium* (*anthodium* Ehrh., *flos compositus* Linn.) A many-flowered capitulum, whose single flowers stand in the axils of more or fewer stunted bracts, and are surrounded with one or more circles of sterile bracts, as in the family of the *Compositæ.*

*b.* The *cœnanthium* Nees, *hypanthodium* Link, exactly like the preceding inflorescence, in some *Urticeacæ.* The cup-shape of the peduncle in *Ficus* is no distinction, since it is wanting in *Dorstenia;* and it exists in some *Compositæ;* the same may be said with regard to the sterile bracts, which are as much stunted in *Dorstenia* as they are clearly present in *Ficus.*

2. The spike (*spica*) in very various forms. The kinds are: —

*a.* The catkin (*amentum*), distinguished by the fact that it falls off entire or by its imperfect flowers. The male inflorescence of *Cupuliferæ, Salicaceæ, Betulineæ,* and some few other plants.

*b.* The spadix. A closely crowded spike, or partially a cylindrical capitulum with fleshy peduncle; in *Aroideæ,* Maize, and some other Grasses, and in Palms, in the last of which it is often compound (*spadix ramosus*).

*c.* The cone (*strobilus* or *conus*). A cylindrical capitulum or solid spike, on which the individual foliar organs become woody scales; as in the *Coniferæ,* the *Casuarinaceæ,* the *Betulineæ,* and some others.

*d.* The spikelet (*spicula*). The simple inflorescence of the Grasses and *Cyperaceæ;* namely, a few-flowered spike, whose flowers have no bracts, surrounded at the basis by one or two sterile bracts (*glumæ*).*

3. The umbel (*umbella*) in the *Umbelliferæ;* when compound termed umbellule (*umbellula*).

4. The raceme (*racemus*) occurs in very different forms; it is usual to distinguish in it —

*a.* The corymb (*corymbus*), a pyramidal raceme.

### *β. Inflorescentia centrifuga.*

5. The cyme or false umbel (*cyma*), a corymb with *inflor. centrifuga.*

N. B. That only singular cases are distinguished in these is a proof of the totally unscientific patching together of terminology. The compound raceme, the compound umbel, and capitulum, with *inflor. centrifuga,* are all called a cyme (*cyma*), which is contrary to the commonest scientific laws. DeCandolle has further

* This, as Link cleverly observed, stands in the same relation to the spike as the *calathium* to the *capitulum.*

applied the term cyme to the inflorescence of the *Boraginaceæ*, which, on account of the peculiar manner in which it unrolls itself, he terms *cyma scorpioides;* and he adds the fiction, that the undermost, first-blooming flower is really the terminal blossom, and the second, the terminal blossom of side axis, is developed in a disproportionate degree, &c. From the rolling up there is just as little to be deduced as from the same phenomenon in the leaves of *Ficus* and *Cycadaceæ*. The position of the bracts, as seen in *Cerinthe*, contradicts this fiction; and the history of the development, which can alone determine the point, appears to me to prove (I own from a few very imperfect observations) that here a one-sided raceme or spike is present, whose unrolling is only a peculiar situation of the buds.

### C. *Once compound Inflorescences.*

#### *a.* Pure or homomorphous.

##### a. *Inflorescentia centripeta.*

6. The spike of the Grasses (*spica*). Several spikes united in a spicate arrangement, as in the Grasses; the component spikes are termed spikelets (*spiculæ*).

7. The umbel (*umbella*); umbels united in umbels; the components are termed umbellules (*umbellulæ*).

N.B. Sound terminology would have long ago rejected these words, and exchanged them for *spica* and *umbella composita.*

8. The panicle (*panicula*); see No. 11.

None of the remaining combinations deserve special names, and may probably be classed among those mentioned under 9 and 11.

##### b. *Inflorescentia centrifuga.*

9. The cyme or false umbel (*cyma*); see No. 5. and No. 14.

10. The *anthela;* see No. 16.

#### *β.* Mixed or heteromorphous.

##### a. *Inflorescentia centrifuga.*

See No. 14.

##### b. *Inflorescentia centripeta.*

See No. 11.

### D. *Many times compound Inflorescences.*

##### a. *Inflorescentia centripeta.*

11. The panicle (*panicula*). Every many-branched inflores-

cence; in Grasses universally, and otherwise only in developed pedicels.

12. The thyrse (*thyrsus*), a panicle, with very short pedicels; with the exception of Grasses, found almost universally.

Both terms are applied also to once compound inflorescences. DeCandolle uses the term *thyrsus* for those in which *inflor. centrifuga* and *centripeta* are mingled; others differently; all arbitrarily.

13. The *anthurus*, an inflorescence that has the kind of aspect of that of the *Amaranthus candatus* or the *Chenopodiaceæ*.

b. *Inflorescentia centrifuga.*

14. The cyme (*cyma*), also in manifold combinations, in which, however, we do not consider whether the side ramifications follow the *inflor. centripeta* or *centrifuga* in longer pedicels.

15. The bunch (*fasciculus*), a manifold compound cyme, with short pedicels, and rather crowded.

16. The *Anthela*, all kinds of inflorescences in the *Junceæ* and *Cyperaceæ*.

17. The glomerule (*glomerulus*), many inflorescences that appear almost like a capitulum, and consist only of ill-formed, imperfect flowers, as in some *Chenopodiaceæ*, *Urticaceæ*, and *Juncaceæ*.

I leave every one with thinking faculties to draw for himself the sad conclusions which the preceding survey affords; and I think that I have not to defend myself to any one who is acquainted with our literature, against the charge that the foregoing is a frivolous vagary of my humour. Röper first *attempted* a scientific development of the inflorescence. No one that I know of has followed him, except Lindley. Physiologists seem not to have accounted it of sufficient importance. Systematists have too much to do with their herbaria, and it is much easier to coin a new word than to study minutely the progressive development through a large series of plants. For the sake of those unacquainted with these matters I will insert the following examples:—In *Lotus corniculatus:* Koch (Syn. Fl. Germ.), a *capitulum*, Kunth (Fl. Berol.), an *umbella*, Reichenbach (Fl. Excurs.), actually a *fasciculus*. To *Eriophorum vaginatum* Kunth gives a *spica;* Koch, a *spicula*. For *Cladium Mariscus* Kunth has *umbellæ axillares et terminales;* Koch, *Anthelæ axillares et termin.;* Reichenbach, *cymæ A. et t.*; in *Isolepis supina:* Koch *spiculis* in *fasciculum aggregatis;* Kunth, *spicis conglomeratis*. I have here omitted the French and English botanists, or the matter would have been still more glaring.

I have also omitted the great crowd of synonymes as altogether useless, and even only introduced the more useful of the names of peculiar inflorescences: otherwise I must have written a whole book upon them, and truly one upon empty words.

## II. *Of the Parts of the Flower at the Time of Blooming.*

§ 144. The flower originates from a bud (*gemma*, here commonly termed *alabastrus*), and is nothing more than a particular modifi-

cation in the perfecting of the parts contained in the bud; namely, the several foliar organs and internodes. It has been already shown, that only two essential processes of development, and from those only two essential organs, as fundamental organs, can exist in the plant; namely, the axis and leaf. All the several parts of the flower must, therefore, be referable to these fundamental organs, and be traced back to them. Since Goethe's time, this tracing back has been termed the Metamorphosis of plants. Originally, this mode of considering the flower rested solely on comparative morphology, and the observation of cases in which the interruption of the usual processes of development, in some or all parts of the flower, caused those parts to reassume forms in which it was not difficult to recognise the nature of the fundamental organ from which they had been produced. This latter has been termed retrogressive metamorphosis; as examples of it, we may mention the different monstrosities, the doubling of a flower through the transition of the stamens into petals, the transition of the petals and sepals into the common leaves of the plant, &c. This mode of establishing the foundations of the doctrine of metamorphosis has, however, two essential faults: since, in the first place, it seeks to obtain individual facts by means of hypotheses and comparisons; while, secondly, its progress depends entirely upon favourable circumstances. The only correct and sure ground on which to rest this doctrine, is the history of development, and this, only quite recently recognised, is as yet pursued by few investigators; hence the doctrine as a whole still exhibits many deficiencies, imperfections, and uncertainties.

The doctrine of the metamorphosis of plants is still partially treated as a special section of Botany, although it is in fact no other than an isolated fragmentary application of the *only really scientific principle* which botany can at present possess; namely, that of progressive development. By most persons, however, the matter was long, by some even still, regarded as an agreeable fantasy, playing round science; the blame of this rested partly upon the manner in which Metamorphosis was introduced into science.

Even Linnæus had a presentiment of something of the kind, and in his Prolepsis Plantarum (Amœnit. Academ. vol. vi. p. 324.) carried it out in such a way, that, starting from the consideration of a perennial plant with regular periodicity of vegetation (as in our forest trees), he explained the collective floral parts from the bracts onward, as the collective foliar product of a five-year old shoot, which, by anticipation and modification, was developed in one year. This view is, in the first place, taken from the most limited point possible—from the examination of a plant of our climate; and, secondly, imagined and carried out with great want of clearness. Up to the formation of the flower in the axil of the bract, the matter holds, perhaps; but from thence the explanation is restricted to the laying down of his untenable, and, in the highest degree, superficial anatomical notions as to the connection of the floral parts with the elements of the stem; and only in a few very indefinite words is it indicated of every floral part, that it (for instance, the stamen)

corresponds to the axillary bud of the preceding (the petal), and no attempt is made to elucidate how it happens that the axillary bud of the calyx appears only as *one* leaf (petal), and yet developes its axillary bud at once, which again is stunted to a single leaf; finally, the usual alternate position of the floral parts, directly contradicting the whole fiction, is not entered into at all.

C. Fr. Wolff (Theoria Generationis, 1764) opened the true and only path by which this doctrine can be carried through, in making good the study of development as the true principle in Botany, as in other sciences. He erred, certainly, in particular conclusions; for instance, in determining the stamens to be modified axillary buds of the petals. But all his intelligent activity remained altogether lost to Botany, a fact readily explained by the scientific spirit of those days.*

Long after Wolff, Goethe wrote his "Versuch, die Metamorphose der Pflanzen zu erklären," (Gotha, 1790), in which he correctly explained most of the floral parts, up to the carpellary leaves, as foliar organs. With his method of mere comparisons and references to monstrosities, he could not, of course, pronounce any thing original and profound as to the structure of the germen. There he introduced, from Schelling's doctrines, the fantastic comparison with an alternating contraction and expansion, from which, in connection with a gradual refinement, proceeded the difference of the parts of the flower. This last was soon dropped. Goethe found little hearing at first in Botany, especially in Germany where the very stupidest materialism of the Linnæan school prevailed; Jussieu and Usteri first mentioned his ideas in scientific Botany. But it was DeCandolle (Organographie, Paris, 1827) who first called general attention to this branch (or rather main trunk) of Botany, and thus the so-called metamorphosis of plants gradually came to its place as a special chapter in the revision of the science. Wolff's ideas were not indicated by a single syllable, at most he was cited with philological profundity as Goethe's predecessor, and thus the whole doctrine, in the absence of the only correct method, remained without any essential influence for the advancement of Botany. As to the import of calyx, corolla, stamen, and carpel as foliar organs all, except a few heretics, were soon agreed. The seed-buds (ovules) were left to originate as buds on the borders of the carpellary leaves, and no great trouble was taken about the thousand contradictions which lay close at hand. The particular families, more complicated in their structure, the pistils of which could not so readily be referred to carpellary leaves, &c., then

* Even now but few botanists have an idea of the importance of the history of development; and while animal physiology progresses with wonderful rapidity through the constant application of the correct method — while in it every rising difference of opinion soon becomes obliterated, because the principle, as to the correctness of which all are agreed, the skill in manipulation, which every one must acquire as an indispensable preparation for profound study, causes every question to be quickly and universally decided — Botany remains hopelessly behind all the sciences. Endless contests about the commonest things consume the best time, and the science moves not; because most botanists either place side by side, as of equal value, or make selections from, without judgment (and take therefore, according to accident, sometimes untruth, sometimes truth), all that is given them by the few inquirers who have taken a higher path. As to critical re-investigation, it is not to be thought of by most. The most important organ in Phanerogamous plants is the anther: how many botanists are there who know the structure of an anther perfectly from their own experience? Hence we find in the books of botanists of the greatest reputation, things stated about the anthers which truly are not a whit better than if J. Müller were to describe the human lungs as simple sacs.

became the tilting-ground for what were in part most adventurous fantasies and fictions. The unfortunate seed which Goethe sowed, sprang up with sad rapidity; and next to Schellingism, we owe it to him * that, in Botany, whims of the imagination have taken the place of earnest and acute scientific investigation. In that unbounded region every individual's imagination had naturally equal right; there was a total want of any scientific principle which should undertake the decision between differing opinions of any method, the recognised accuracy of which could give security for the results of an investigation.

I have striven, in my methodological introduction, to develope such a principle for Botany, out of the contemplation of its object; and I here once more express my firm conviction, that without rigid carrying through of the investigation of development, in the total as in the singular, Botany is, and will remain, an unscientific game of purely arbitrary arrangement and combination of uncomprehended forms. In spite of our by far less difficult problem, Zoology has far outstripped us, and has shown us the road which properly she should have learned from us. We must follow behind, if every botanist does not in time become red with shame, who takes in hand a work of Müller, Schwann, Reichert, Baer, Rathke, Siebold, Wagner, and all the hundred others, by the side of whom we can scarce place half a dozen.

Following Robert Brown, I first sought to apply the investigation of development to the discovery of the structure of flowers. In this manner I found the explanation of the flower of the Grasses, the Carices, the composition of the involucre in *Euphorbia*, &c. With my deceased friend Vogel, I published the first perfect history of development of the flower of a *Leguminosa*. After a considerable time some botanists followed

* Perhaps a part of the blame rests upon an innocent encouragement, expressed in a friendly manner, in a letter of A. von Humboldt, who certainly did not mean what Goethe understood him to do, at a time when, from his total want of mathematical experience and knowledge, he made such a poor figure in science with his theory of colour. Goethe said (Contribution to Morphology, Stuttgard and Tübingen, 1817, p. 122.):— "Humboldt sends me his work with a flattering picture, by which he indicates that poetry may indeed attain to lifting the veil of Nature; and if he admits it, who will deny it?" Humboldt certainly meant no more by this than that a poet, who by his inmost nature is led to it, may, in particular cases, conceive the universal (that is, the universal human), and even may succeed, by the contemplation of Nature alone, in finding a happy thought, without that thought itself being already science, and without admitting the possibility of its becoming an integrant part of it until further carried out and investigated. The mistaken meaning which Goethe attributed to the words, that a poetic treatment of nature could be placed on a level, or even preferred, to the rigidly scientific, could not have existed in Humboldt's mind. But it happened just at a time when the misty fanaticism of Schelling's "Philosophy of Nature," built on the same want of psychological investigation, stirred up together imagination and intellect, musings and thought, poetry and science, into a mixture as distasteful to the true poet as to the clear thinker. This has brought much trouble upon us in science, and, especially in Botany, caused a gnawing disease of development. Zoology soon recovered from this fever, since it had at that time already developed abundance of healthy juices; but Botany, which then was staggering about as the melancholy Linnæan skeleton, had longer to suffer; since, judging from the preceding condition, the ruddy hue of fever was taken for a sign of health. Poetry and science are two regions distinct in their inmost essence, which both lose their whole value when they are intermingled. A poetical treatment of science, and especially of philosophy, the most strict of all sciences, is as repugnant and distasteful to the clearly educated mind, as if one should strike a bargain, order a coat, or call a servant in a poetical speech. A learned poem is empty versified prose — a remnant of the barbarism of the middle ages — poetical science is a troubled mysticism of a cloudy fanatic, of whom, indeed, in the imperfect education of our thinking powers in youth, there will long exist instances.

me, and have in part confirmed the correctness of my views. The first was Geleznoff in *Tradescantia virginica* (Bull. de la Soc. Imp. des Nat. de Moscau, tom. xvi. 1843). He was still doubtful whether the stamens did not arise earlier than the corolla. Duchartre spoke more decidedly on this point, with regard to the *Malvaceæ* (Compte rendu, 1844, séance 18 Mars), and the *Primulaceæ* (ibid. séance, 18 Juin). On the other hand, Barnéoud confirmed my observations completely, through the investigation of the *Plantaginaceæ* and *Plumbaginaceæ* (Compte rendu, 1844, 30 Juli). Strangely, he says *, that the course of development of the flower follows, against my theory (!), *from without inwards*, which on account of the figures given by Vogel and myself, cannot be excused, even on the plea of ignorance of the German language.

It has often been attempted to develope the morphological laws of the structure of flowers from monstrous formations. I believe that this attempt is altogether faulty, even presupposes a total ignorance of the value and import of the progressive development. If up to this point one must reject every application of the analogy of animals to plants, it were yet very desirable that most botanists should go through a thorough course of zoological physiology, so that they might, at least in some degree, learn method in the treatment of organic bodies. Whoever has traced the course of development of even a couple of only rather difficult flowers, will have certainly become convinced that every conclusion from the developed flower as to its regular rudiments, and the import of its parts, must inevitably be faulty, and that monstrosities, double and proliferous flowers, such as are transformed into leaves, &c., require elucidation by the history of development just as much as the normally formed flower itself. Even Mohl might have spared himself his so acutely carried out examination of *Poa vivipara*, and the explanation of the flower of Grasses deduced from it (Botan. Zeit. b. iii. p. 33), if he had only convinced himself, in the flower of a single Grass or of a single *Carex*, how by a subsequent one-sided development, the most perfect symmetry becomes wholly hidden. I have thought myself obliged, especially for a better understanding of the importance of the course of development, to care for it in publishing several of the more difficult or more instructive instances in the accompanying plates; namely, in Plate III. the course of development of the leaf of *Pisum sativum*, of the flower of *Agrostis alba*, of *Carex Lagopodioides* and *Canna exigua*; and in Plates IV. and V. a more complete illustration of the development of the flower of *Passiflora princeps*.

§ 145. In Phanerogamic flowers the following parts are distinguished, proceeding from without inwards: 1. The floral envelopes, as the external calyx (*epicalyx*), of which the parts are leaves (*phylla*); the calyx, the parts of which are sepals; the corolla, the separate portions of which are petals; or, instead of these three, the perianth (*perianthium*), whose separate parts are leaves (*phylla*): 2. The stamens (*stamina*), around and within which some stunted accessory foliar organs appear under very various names: and, lastly, 3. In the centre of the flower, the pistil (*pistillum*), the separate foliar organs of which are carpels (*carpella*). In the stamens the lower thread-like portion, which is termed the filament (*filamen-*

* At least in the extract in the Botanische Zeitung, 1845, p. 115.

*tum*), is distinguished from the upper thick and hollow part, containing the dust (*pollen*), called the anther (*anthera*). In the pistil, the lower part surrounding the seed-buds (*gemmulæ*) is called the germen*; the upper free part, which is usually covered with *papillæ*, is termed the stigma, and between these two frequently a stalk-like elongation of the germen occurs, called the style.

The flower of *Phanerogamia* is the only physiologically determinate organ of the plant, since it contains the apparatus for the regular propagation. But to this only two forms contribute: namely, the stamens, as generators and receptacles of the pollen; and the seed-bud, as the place in which the pollen is developed into the embryo. All the remaining parts of the flower; namely, the envelopes of the whole perianth, the calyx, and corolla, the receptacles containing the seed-bud (the germens, styles, and stigma), are not, in a physiological sense, essential, and they may be absent, without the flower losing its correspondence to the character by which a flower is defined.

In the correct (morphological) view of the flower, there is no distinction between essential and inessential forms, and, therefore, it is necessarily more proper to divide into axial and foliar organs. The following relations of condition must be borne in mind: — The axis and its modifications are the basis of the flower, because to them the foliar organs are attached. Attached to the outer part of the axis of the flower occur several forms of true foliar organs, the floral envelopes, accessory leaflets, and stamens. The innermost part is occupied by organs which are formed from true axial organs, or an intimate blending of these with foliar organs, which are termed the female apparatus, or, better, the rudiment of the fruit. At the same time, the parts of the flower are usefully grouped together and treated generally, according to the relations of number and position, as well as of duration; thus we obtain this plan for our following investigations: —

*A.* The axial organs of the flower.

*B.* The number, relative position, and duration of the parts of the flower.

*C.* The true foliar organs of the flower.

*a.* The floral envelopes.

*b.* The stamens.

* The term hitherto most frequently applied to the seed-bud is *ovule*. In the first volume of the first edition of this work I proposed that botanists should agree to banish from their science all expressions which have a definite signification in Zoology, so that for the future we might avoid the continual confusion which so readily arises through the conceptions obscurely introduced from that science. With pleasure I saw that a better man than myself, A. Endlicher, had been before me in this in his "Enchiridion Botanicum," and throwing aside the term *ovulum*, had substituted for it *gemmula*; and, instead of the customary expression *ovarium*, had used the old word *germen* for the lowest portion of the pistil. I follow him here, and believe that I have translated the word *gemmula* tolerably closely by seed-bud (Samenknospe); on the other hand, I retain, from the many expressions substituted for the usual name of *placenta* for the part bearing the seed (Samenträger), the term *spermophorum* in preference to *trophospermium*, which is grammatically incorrect in its construction, and, signifying more, is not so applicable to the purpose.

*c.* The accessory foliar organs.
*D.* The rudimentary fruit.
*a.* Of the pistil.
*b.* Of the spermophore.
*c.* Of the seed-buds.

Hitherto the anthers have been called the male organs of a plant (with the superfluous collective term *andrœceum*); the seed-buds and their receptacle the pistil, the female parts (together the *gynœceum*). A flower that contains both parts is termed hermaphrodite (*flos hermaphroditus*); flowers that contain only one of those kinds of organs, are termed unisexual flowers (*flores unisexuales, diclini*). When, in the last case, male and female flowers (*mas et femina*) appear on the same individual plant, such plant is termed monœcious (*planta monoica*); when they appear on separate individuals, the plant is termed diœcious (*planta dioica*). An inflorescence which contains both male and female flowers, also is termed *inflorescentia androgyna*. Here again it must be distinguished whether the male and female blooms are formed upon different plans, as in the *Cupuliferæ* (*true diclines*); or whether, through the suppression of one or other part, a pseudo-diclinous condition appears in a flower formed on the plan of a hermaphrodite. This latter condition, which is never found to run through all the examples of any species of plant, brings monœcious and diœcious species into hermaphrodite genera, and suggested to Linnæus the establishment of his twenty-third class, *Polygamia*, where in one and the same species male, female, and hermophrodite flowers are present.

Very incorrectly, the pistil, as the receptacle of the seed-buds, and as the apparatus to facilitate impregnation, is usually counted among the essential parts of the flower; for it may be absent as well as the floral envelopes, as in the *Coniferæ, Cycadaceæ*, and *Loranthaceæ*, which have a naked seed-bud. The simplest form of the flower is that in which only a few foliar organs are converted into anthers, and between them the simple extremity of the axis displays itself as the simplest form of seed-bud. We might reckon as exactly such an ideal flower (primary flower) that of *Viscum album* (fig. 180.), were not the true condition interfered with here by the fact, that some examples constantly develope only anthers, the seed-bud not being perfected for its function; whilst upon others the axis alone is perfected into the seed-bud in its most simple form, and the four foliar organs persist around it in the condition of leaves. Further, I have to observe, with respect to *Viscum*, that there is

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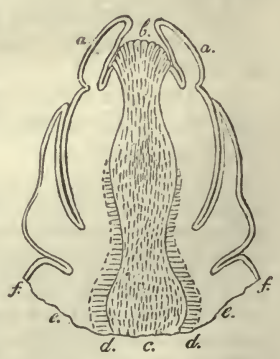
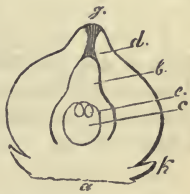



[180] *Viscum album.* Vertical section of the female flower. *a a*, Leaves of the floral envelope; *b*, naked seed-bud, consisting solely of the naked nucleus, and formed from

not yet any distinction or division of the axis as pedicel from the axis as seed-bud. The axis terminates immediately in the flower, with a scarcely evident rounding of the extremity, and all that gives it peculiar import to the seed-bud, namely, the formation of the embryo-sac, as well as the subsequent development of the embryo, is carried on in that part of the axis beneath the flower, therefore in the pedicel. The term *gemmula infera* would in fact be applicable here. Amongst the *Coniferæ*, the female flower of *Taxus* (fig. 180*a*.) is an example of the simplest structure; here, again, we see nothing of floral envelopes or seed-vessels, but the seed-bud no longer exists in the simplest form, as a naked nucleus (*nucleus nudus*); it has a coat (*integumentum*), but no germen, and therefore it is still always a naked seed-bud (*gemmula nuda*).*

180 *a*




The distribution into essential and unessential parts of the flower is, according to my manner of treating the matter, entirely useless. For the morphological consideration of the plant each organ is equally essential, as a definite expression of the form-creating power of the plant, and it is in this point of view unimportant, whether or not the part fulfil some determinate function, or what this be. In the morphological treatment of the flower the only correct division is into axial and foliar organs; but I must not carry out this reform with unvarying strictness, lest I depart too far from the old beaten track, and thus, perhaps, become, if not incomprehensible, yet apparently too difficult, although in fact the development of the flower would thus become far more simple, and be freed from innumerable, otherwise inevitable, repetitions. In the almost total neglect, too, of investigation of development, any other than the usual mode of treatment has been hitherto impossible.

There are a few more points to notice. Since the time of Linnæus it has been usual to class the nectaries with the parts of the flower characterised by the secretion of a fluid containing much sugar. This characteristic was subsequently laid aside and more regard paid to its external form, so that at last all possible things have been gathered together under this name. If we would really comprehend the structure of the flower,

* Link (Linnæa, vol. xv. 1841 (!), p. 482.), with the appearance of great acuteness, remarks, against Robert Brown's view of the structure of the Coniferous flower, "Si ad micropylen apertam respicis semen nudum dicere poteris, si vero ad integumenta (ex quo stigmata duo excedunt) tectum erit." Had Link more than hastily skimmed the writings of Robert Brown, Brogniart, and Mirbel, he would have known that they very strictly distinguish a *gemmula nuda* from a *nucleus nudus*. According to the common use of language, an organ is *nudus* which wants the *immediately succeeding* covering; the nucleus, therefore, is *nudus* without the *integumentum;* the *gemmula*, without the *germen*. *Semen* means nucleus and coats together, and can only be called naked when no *pericarpium* exists; but it is the *gemmula* which is under consideration here: the micropyle is a part of the coat of the seed-bud; the stigma, a part of the pistil. Either the integument of the *nucleus* in the *Coniferæ* is a coat of the seed-bud — then it is absurd to talk of a stigma, — or it is a *germen*, and then no micropyle exists. But I must return to this hereafter.

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the somewhat hemispherical projecting extremity of the stem; *c*, pith, within the middle expanded portion of which some cells are transformed into embryo-sacs; *d*, circle of vascular bundles; *e*, bark; *f*, epidermis.

[180a] *Taxus baccata.* Vertical section of the seed-bud. *a*, Base and point of attachment of the seed-bud; *b*, nucleus; *c*, embryo-sac; *d*, simple integument; *e*, large cells of the endosperm (*corpuscula*, Robt. Brown); *g*, micropyle; *h*, rudiment of the coat of the seed.

we must distinguish first of all axial and foliar organs, and then independent organs and mere appendages and excrescences of particular organs. In all these parts it may, and sometimes does, happen, that a part of the surface does not develope epidermis, and secretes a saccharine or often other kind of juice. Neither the wholly subordinate and always accidental condition of structure, nor the function, and this least of all, justifies the assumption of its being a special organ. To define nectaries according to form has not been attempted, and would, indeed, be an impossibility. I reject the term from morphology, as altogether useless.

### A. Of the Axial Organs of the Flower.

§ 146. There are very few flowers of so simple a structure that they consist only of one simple essential part, so that no formation of internodes is possible within the flower; and the extremity of the pedicels immediately supports the floral parts existing. This is the case in the male flower of the *Euphorbiæ*, where the end of a pedicel bears one single stamen; also in the male flower of the *Abietineæ*, where one single foliar organ, converted into a stamen, constitutes the entire flower: it is the case in the female flower *Taxus*, where the small pedicel, clothed with bracts, terminates immediately in the naked seed-bud. In the generality of flowers, however, several parts are united which do not stand at equal heights on the axis, and thus more or fewer internodes take part in the structure of the flower. The original condition of the internodes, the undeveloped, is here also most frequently permanent; and the pedicel, after the detachment of all the parts of the flower, frequently ends in a small, slightly thickened knot, which represents the collective internodes of the flower in undeveloped condition, the simple base or receptacle of the flower (*torus*). Examples in which individual internodes become elongated are rather rare. I am not acquainted with any case where this occurs between the floral envelopes, but in some families they are elongated between the inner floral envelopes and the stamens (*androphorum*), and between the stamens and the germen (*gynophorum*). The latter is generally termed *germen stipitatum*. There are examples of both in the *Passifloræ* and the *Capparideæ*.

A considerably longer part, without elongation of the individual internodes, frequently occurs as a gynophore in flowers which contain many germens (as in the *Rosaceæ*, the *Ranunculaceæ*, *Magnoliaceæ*, &c. Again, the gynophore is often presented as a hemispherical or cushion-like part, as in some other *Rosaceæ* and *Ranunculaceæ*; a very rare form of it is that of a reversed cone, which bears the germens upon a base turned upward, as in *Nelumbium*. In the rarest instances, with the exception of this case, the axis of the flower is elongated within the floral parts, even without ending as a germen; but this does sometimes occur as in the male flowers of some Palms and other plants; for ex-

ample, *Chamædorea*, where the points of the petals unite with the apex of the axis of the flower which passes up through them.*

In very crowded inflorescences, the torus of an axillary bud developes obliquely, and rises up on one side, especially beneath the germen, so as to appear as a part of its side-wall; this happens with most of the Grasses. A similar circumstance, arising from a similar cause, happens when many single germens are present in one flower, by the division of the torus, which forms the basis of each of those germens, and thus assumes the appearance of forming a part of the wall of the germen (as in *Potamogeton* and *Dryadeæ*).

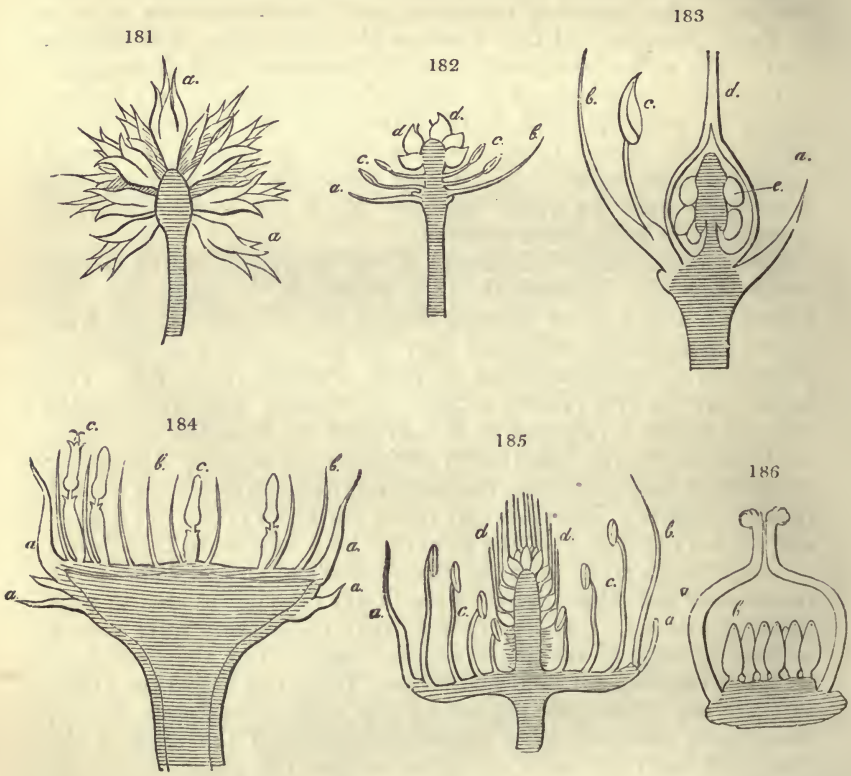
But the development of the internodes into a disc, or in a hollow cup, is far more frequent in the flower. If the collective internodes of the flower form a hollow body, or even a cylindrical elongated tube, which encloses *only* seed-buds, and bears *all* the floral parts upon its upper edge, all this is the so-called inferior germen, or ovary (*germen inferum*).

Every other similar expansion of the internodes of the flowers which does not immediately bear seed-buds, is called the disc (*discus*). This may be situated beneath the rudiment of the fruit (*discus hypogynus*), and then may be flat, as in *Potentilla* and *Fragaria;* or cup-shaped, as in *Rosa*, *Populus* (*mas*), &c. This latter may be free (*Rosa*), or may be blended with the germen situated inside it (*Pyrus*), or it may pass off from the middle of the (half-inferior) germen (*discus perigynus*), as in many *Myrtaceæ;* or, lastly, it may rise above the (inferior) germen, and stand upon it (*discus epigynus*). Here it is very rarely (or never?) flat, but funnel-shaped, as in *Godetia;* in the form of a long tube, as in *Œnothera;* or resembling a style, as in the *Orchidaceæ* and *Aristolochiaceæ*. In these cases, the foliar organs of the flower may be situated in very different places. Usually, indeed, they collectively form a zone around the edge of the flat or concave discs; then the discs may be said to correspond to as many discs, lying one above the other, as there are internodes implied by the number of foliar organs. Frequently the true foliar organs stand around the edge of the disc; and upon its inner or upper surface the germens are arranged in one or more circles (as in *Rosa*, *Punica*, *Onagraceæ*). More rarely the floral envelopes alone stand on the border, while the stamens are then at a distance from them, upon an internal prolongation of the disc, as in the *Orchidaceæ*.

The disc is by no means always regularly developed, but sometimes enlarged at one side only, whereby the whole flower appears oblique, thus in *Reseda*. The most remarkable structure is in *Pelargonium*, where the disc forms a cavity to one side of the peduncle, and in *Tropæolum*, where the spur is formed solely by the disc.

* Here, and in some similar cases, this portion of the axis is falsely called an abortive germen. The germen in these cases is usually composed of carpels, and these never exist in an abortive condition. The spermophore differs from the axis *solely* through the presence of the seed-buds, and therefore neither does it exist here.

There are but few special observations to be made respecting the structure of the internodes of the flower; it is in general like that of annual stems; but it must be remarked that they often possess fewer vascular bundles, and these of simpler development. It is more particularly to be mentioned, that the internodes (as also some of the foliar organs) within the flower, frequently do




[181] *Echinops ruthenica.* A capitulum with flower-buds (*a*), in vertical section. The shady part is the axial organ (the peduncle).

[182] *Ranunculus procerus.* A flower in vertical section. *a*, Calyx; *b*, corolla; *c*, stamens; *d*, carpels. The shaded part is the axial organ (peduncle, *torus*).

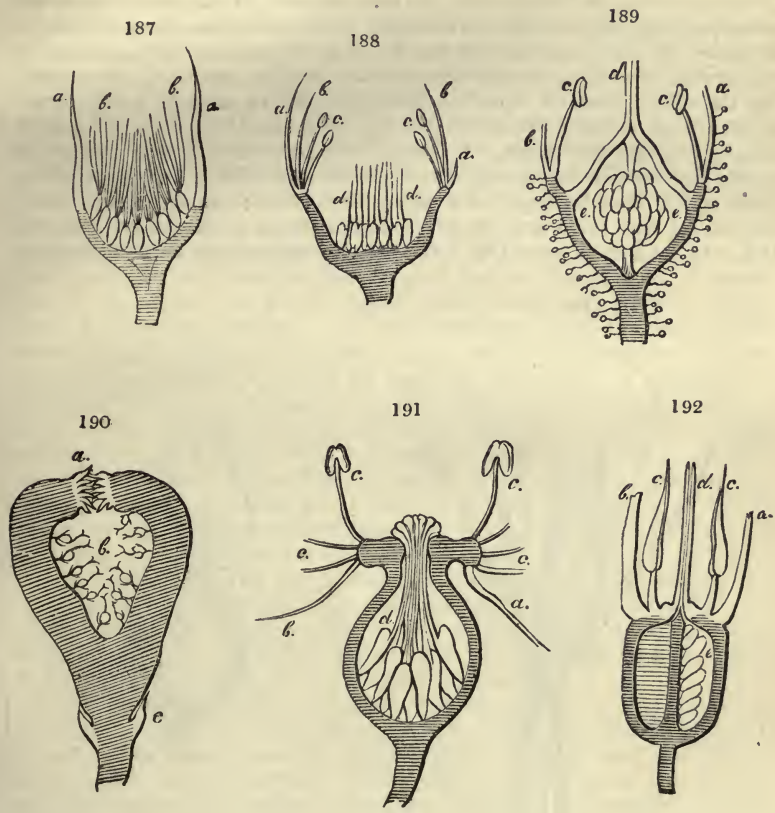
[183] *Ephemerum Matthioli.* A flower, in vertical section. *a*, Calyx; *b*, corolla; *c*, stamens; *d*, carpels, forming the germen, pistil, and stigma (which is cut off); *e*, seed-bud. The shaded part is the axial organ (spermophore).

[184] *Helianthus annuus.* A capitulum in vertical section. *a*, Leaves of the involucre; *b*, bracts (*paleæ*); *c*, flowers. The shaded part is the axial organ (discoid peduncle).

[185] *Geum rivale.* Flower in vertical section. *a*, Calyx; *b*, corolla; *c*, stamens; *d*, carpels. The shaded part is the axial organ (discoid receptacle-disc), and in its centre a gynophore.

[186] *Arisarum australe.* Pistil in vertical section. *a*, Carpels, forming the side walls and covering of the germen, the style, and the stigma; *b*, seed-buds. The shaded part is the axial organ (discoid spermophore), forming at the same time the base of the germen.

not have the epidermis developed, but, instead of this, a delicate, soft, cellular tissue, somewhat yellowish in colour, and often containing a sugary secretion, forms the investment of the surface (*Nectarium*).




[187] *Sonchus asper.* A capitulum past flowering, in vertical section. *a*, Involucral leaves; *b*, half-ripe fruits, crowned with the hair-like calyx (pappus). The shaded part is the axial organ (cup-shaped, concave peduncle).

[188] *Dryas octopetala.* Flower in vertical section. *a*, Calyx; *b*, corolla; *c*, stamens; *d*, carpels. The shaded part is the axial organ (cup-shaped, concave receptacle-disc).

[189] *Heuchera villosa.* Flower in vertical section. *a*, Calyx; *b*, corolla; *c*, stamens; *d*, carpels, forming the covering of the germen and the style; *e*, seed-buds. The shaded part is the axial organ, forming the base and side-walls of the germen and a narrow perigynous disc.

[190] *Ficus carica.* Capitulum in vertical section. *a*, Leaves of the proper involucre; *b*, flowers; *c*, leaves of the outer involucre. The shaded part is the axial organ (vase-shaped peduncle).

[191] *Rosa davurica.* Flower in vertical section. *a*, Calyx; *b*, corolla; *c*, stamens; *d*, carpels. The shaded part is the axial organ (vase-shaped receptacle-disc).

[192] *Leucojum vernum.* Flower in vertical section. *a*, Calyx; *b*, petals; *c*, stamens; *d*, carpels, at present only forming the style and stigma; *e*, seed-buds. The shaded part is the axial organ (an inferior germen).

With the so crowded structures and the many blendings of organs in the flower, it was not easy to comprehend clearly the conditions described in the paragraphs; and of all the parts of the flower, these structures have been the latest that we have come to understand. It seems easiest to comprehend them when we place in parallel rows, side by side, the various forms which the axis assumes, as has been done in the accompanying figures (figs. 181—192.). We here trace the axis from a simple round swelling, through the flat disc, the concave disc, and until it reaches the form of a vase, and this in three parallel series; the first bearing the entire blossom (figs. 181. 184. 187. 190.); another bearing germens, that is, carpels and seed-buds (figs. 182. 185. 188. 191.); and a third simply bearing seed-buds, or immediately surrounding the cavity in which the seed-buds occur (figs. 183. 186. 189. 192.). I know of no form which would carry the first series further; on the other hand, the second and third are not properly completed without figs. 193. and 194. In the first of these (fig. 192.) the cup-shaped disk is carried up be-

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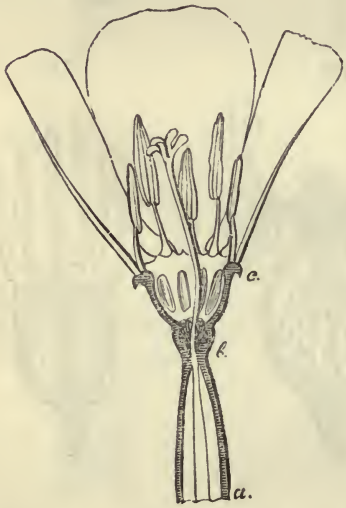


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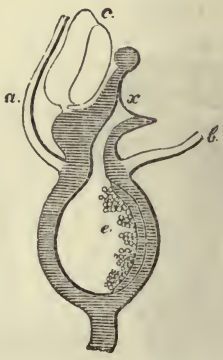


yond the upper part of a vase-shaped closed axial organ, in the form of a new disc. By the extension of the same in fig. 194., on the contrary, the part, which in the remaining members of the series is always formed of the foliar organs, is here drawn within the circle of the axial

[193] *Godetia Lehmanniana.* Flower in vertical section, upper part. The shaded part is the axial organ. From *a* to *b* is the inferior germen (fig. 192.); from *b* to *c* is the superior cup-shaped disc (fig. 188.). This superior disc exhibits elegant projecting portions, quite similar in kind to those on the inferior disc of *Passiflora*, only less developed. (See Plate III.)

[194] *Epipactis latifolia.* Vertical section through the flower. *a*, External; *b*, internal leaves of the perianth; *c*, stamens; *e*, seed-buds; *x*, stigma. The shaded part is the axial organ; the under part, up to the insertion of *a* and *b*, is the inferior germen; the upper part is originally an androphore, then a gynophore; but the carpels are wholly abortive, and the axis itself forms the style with these last parts above *a* and *b*

organs, namely, the style and stigma. Then, to create all possible combinations, comes the interesting structure of *Siphonodon celastrineus*, described by Griffiths in the Calcutta Journal, where the carpels form the cavity of the germen and the canal of the style; while the axial organ forms the spermophore, the conducting cellular tissue, and the large umbrella-shaped stigma.

All those structures grouped together under the name of discs in the paragraphs are doubtless of the same nature; the development distinctly shows them to be flat or concave expansions of the internodes entering into the flower; sufficient analogies to which occur in the flat undoubted internodes of many Compositæ (e. g., *Helianthus*, fig. 184.), in the hollow ones of *Ficus* (fig. 190.), and so forth. The assertion of the axial nature of all the structures mentioned is, in remarkable manner, inductively proved by the following considerations; that one leaf actually springs from another, grows forth from it, contradicts the definition, and is therefore impossible. The assumption of a calyx-tube, therefore, of blended foliar organs in the *Onagraceæ*, *Rosaceæ*, &c., from which free petals should spring, was altogether an unconsidered and absurd fiction. An axial structure must necessarily have been presupposed here; and then it was completely unwarrantable, and clumsy prolixity, to superadd an imagined coherence of sepals into a tube, and adherence of this tube to the discoid receptacle, for instance, in *Rosa* (fig. 191.), *Geum* (fig. 185.), &c. (while not the most distant attempt to demonstrate such a condition was thought of). In these cases (the so-called *Calycifloræ*) the sepals are no more grown together than the petals, and they stand quite free upon the border of the inferior (fig. 185.), surrounding (figs. 188. 191.), or superior disc. But the course of development speaks with equal decision in favour of the view propounded in the paragraphs, since often the structures, and especially the inferior germen, exist complete, or almost so, and at least clearly perceptible, before even a trace of the leaves which grow out of them is evident. (See, in regard to this, the development of the flower of *Canna exigua*, Plate III., with the explanation.)

In all discs, the sudden change of texture, and commonly also a distinctly projecting rim, show the boundary of the disc, and the point of connection between it and the foliar organs standing upon it; and by these marks, in the generality of *Calycifloræ*, the calyx is characterised as composed of free foliar organs not coherent by growth. I recall it to recollection here that, in these forms of the axis, the middle of the lower or outer surface corresponds to the lowest portions of the axis, the lower or outer and the upper or inner surfaces, together, to the sides of the axis, and the central point of the upper or inner surface to the apex of the axis. On this axis the individual foliar organs, or circles of leaves, may be very variously arranged, as is seen by comparing together figs. 188. 191. 193. It is not necessary that they should be all attached around in one zone, for in the discoid axis a condition is possible which, as in the elongation of the axis, separates the individual foliar organs or circles from one another, and corresponds to one or more developed internodes. It is usual for all internodes of the flower to concur in the formation of the discs where this exists; but there are cases where this is not so, and where the different internodes assume very different forms. Thus the *Rosaceæ* are divided pretty strictly into two groups, according as the disc is quite flat or concave (*Rosa*, *Sanguisorbeæ*, figs. 188. 191.), or the internodes between calyx and stamens

flat, and those between the germens hemispherical or conical, convex (the remaining *Rosaceæ*, fig. 185.). Yet more striking is the difference in *Passiflora*, where a flat disc bears upon its edge the calyx and corolla, whilst the internode between this and the stamens is elongated in its upper part, and that between the stamens and the germens in its whole extent (Plate IV.).

Sometimes individual internodes of the flower appear strikingly developed; this most frequently occurs in the gynophore, in the *Labiatæ* and *Boraginaceæ*, as a thick fleshy disc (*gynobasis*); in the *Malvaceæ* as a thick, conical body, bearing the circle of germens; in *Ranunculaceæ* (e. g., *Myosurus*) and in *Magnoliaceæ* as a long, almost cylindrical, organ.*

No word has been so falsely used as the word *discus;* all the peculiar organs found in the flower, which could not be reduced to the four common forms — calyx, corolla, stamen, or pistil — have been heaped together under the term *discus.* Thus in the *Thymeleaceæ* decided, even perfectly free, foliar organs; in the *Scrophularineæ* and allied families, a circle of coherent foliar organs (termed also *annulus hypogynus*); in the *Umbelliferæ*, the somewhat fleshly and succulently developed lower part of the carpels (as *discus epigynus*); and the like. An infinity of special conditions still remain to be investigated and explained; I can only offer the few which I have had time to examine; a complete working out of these conditions would be a most meritorious task, and would be of infinite assistance in the recognition of natural affinities; but one must not restrict oneself to calling a *discus* every yellow and rather succulent body one finds in the flower.

I cannot repress here a teleological observation, which I own is not scientific. We do find the discoid and cup-like form in other axial organs, but nowhere so frequently as in the internodes of the flower: this is, however, unquestionably the simplest means to produce a condition of things favourable to a great multiplicity of structures, without injury to the dimensional connection and apparent individuality and completeness of the flower.

### B. Number, relative Position, and Duration of the Parts of the Flower.

§ 147. It is very rarely that a flower consists of one part only, as in the male flowers of *Euphorbia*†, *Lemna*, and *Wolffia*, which are formed of one foliar organ, the anther; or the female flower of *Taxus*, which is formed of one axial organ, the seed-bud. Usually more parts unite to form a flower: thus the female flower of most of the *Aroideæ* consists of one or more seed-buds, and a carpel surrounding them. The male flower of the *Salicineæ* consists of a scale-like disk and several stamens. In the generality of cases, male and female organs are both present in the same flower: they are seldom naked, as in *Hippuris*, but usually surrounded by floral envelopes.

* Analogous to the disc in the *Boragineæ* and *Labiatæ*, the axis in the *Cruciferæ* and *Alsineæ* forms tumefactions on the base of the stamens, which surround the bottom of the pistil as little scales or a little cup, and are usually described as inferior glands, because they often secrete sweet viscid fluid through the epithelium, which remains very delicate.

† Here the single stamen (foliar organ) stands exactly on the middle and the end of the little pedicel. A complete history of the development is still a desideratum.

In axillary flowers, those parts which are turned towards the peduncle are termed the upper, and those turned towards the bract, where it is present, the lower. Some plants exhibit the peculiarity, that the pedicel, until the time of the blooming, makes a half turn (analogously to the twining stem), and it may be the true pedicel, as in *Calceolaria* and some *Orchidaceæ;* or the inferior germ, as in most of the *Orchidaceæ.* By this curve, the upper parts of such a flower (in those plants the *lip*) become apparently the under; and such flowers are termed *flores resupinati.* The term is sometimes falsely applied to those *Orchidaceæ* in which no such twisting takes place, but in which the lip stands regularly as the upper part of the flower, as, for example, in *Epipogium.*

The individual organs of the flower taken generally, according to the common view, and known by collective names, may originally consist either of one piece or of more than one: in the first case they are *partes monomeræ;* in the second case *partes di-, tri-,* or *polymeræ.* In the latter case the parts may be entirely separated and independent of one another, or they may be grown together in various ways. These coherent sets were formerly also called *partes monomeræ.* De Candolle better termed them *partes gamomeræ;* as, for example, *Hemerocallis* = *perianthium gamo-* (*mono-*) *phyllum, hexamerum; Salvia corolla gamo-* (*mono-*) *petala pentamera; Rosa corolla pentapetala,* &c.

The coherence occurs here in the same manner as in the stem-leaves, but, on account of the crowded position in the flower-bud, much more frequently. It happens either so that a single foliar organ grows together by its edges into a tubular or cup-like organ, as, for example, occurs frequently in the so-called monomerous floral envelope (bracteole); or that several foliar organs grow together by their edges: this commonly affects all the edges of a circle of leaves, but sometimes two edges remain ununited, as with the calyx of *Gentiana lutea.* So, again, this process is usually simultaneous in development at all the edges of a circle; but it sometimes happens very much later — *a.* on two uppermost leaf-edges, whereby the single-lipped forms arise, as in the corolla of *Teucrium* and the *flores ligulati* of the *Compositæ;* or, *b.* with each pair of leaf-edges at the side of the leaf-circle, whereby the two lipped forms (*part. bilabiatæ*) of descriptive botany arise. Another kind of blending also occurs in the flower, of which I know no example in the stem-leaves, and only one in the bracts and bracteoles, namely, the *cupula* of the *Cupuliferæ,* this is the blending together of two or more circles, as in the two circles of the floral envelopes of many *Liliaceæ;* or in these and the two circles of stamens, in the circle of petals and stamens, in the *Labiatæ,* &c.; and in general in all flowers to which are ascribed *stamina perianthio vel corollæ* (not *calyci*) *inserta.*

The coherence of the stamens of one or more circles has been well termed, since Linnæus' time, fraternity (*adelphia*), and, according to the number of brotherhoods in a flower, *mon-*

*adelphia, diadelphia, polyadelphia.* When the foliar organs of the flower are coherent, the blended part is termed the tube (*tubus perianthii, calycis, corollæ,* &c.); the free parts, the limb (*limbus*); and the boundary of the two, the throat (*faux*). One of the most striking examples of coherence, which also has no analogue in the stem-leaves, is found in the blending of the foliar organs of the flower at the point only, the union never extending further; so that the foliar organs are connected above, but free below, as in the corolla of the male flowers of *Chamædorea, Casuarina,* and in the androphore of *Symphyonema montanum* (?).*

Abortion in the flower has the same and simple meaning which I have explained at length in the case of the foliaceous organs; namely, that some part present in the rudimentary condition is arrested in development, and during the gradual perfecting of the flower, and thus at last retires from observation. The assumption of any other kind of abortion has no place in natural science; it is a mere dream of the imagination. So soon as the individual parts of a flower become distinct members, the foliar organs appear arranged around an ideal and real axis of the flower (the axial organs of the flower), and in the rudimentary condition always regularly. Through subsequent unequal development of the single parts the flower frequently becomes symmetrical, or, as it is called, irregular. This irregularity is always such, that the upper part of a flower becomes developed differently from the under. Such irregularity very seldom affects the germen, which almost universally remains regular, even in symmetrical flowers; yet there are cases in which this is the only symmetrical part, as in many of the *Scrophulariaceæ, Acanthaceæ,* and *Cryptocoryne spiralis.* If the symmetrical flower, with or without coherence of its parts, is divided into two halves, an upper and under, developed in different ways, they are generally termed bilabiate; but if only one single foliar organ is developed in an aberrant form, that leaf acquires the name of *labellum,* or lip. Rare, indeed, are the cases where the entire flower is unsymmetrical, as in *Goodyera discolor.*

It is not possible to state, in general terms, the number of parts which may unite to form a flower. We find, of foliar organs alone, sometimes so many as fifty or sixty united in one flower. Certain combinations, on the contrary, are rarely met with: I know of no monomerous flower possessed of double floral envelopes. When the various parts of the flower are present in large numbers, these arise universally, in one or more circles (whorls), at the same height on the axis, and at the same time. When circles containing members of equal number follow in succession, the members of the one circle usually stand opposite the interspaces between the members of the preceding circle (the circles and their members alternating); they seldom stand precisely before

* Other conditions, such as the connection of the points of the two outer petals in the *Fumariaceæ,* of the anthers in the *Compositæ,* &c. do not belong here. These are glued together by a fluid secretion.

them (the circles and their members opposite). But it by no means is to be assumed that the members of each circle are always of equal number in a flower. The number of members often increases up to the stamens, and from thence diminishes: it is rare for the circle of the carpel to contain the greatest number, as in the *Malopeæ* and *Malvaceæ*. The generality of Monocotyledons with perfect individual flowers* have regular homomerous circles through the entire flower: in the Dicotyledons this is relatively rarer; the outermost and innermost circles have usually fewer members. Again, respecting the number of circles which follow one another, no general statement of importance can be given. Seven different forms of foliar organs may possibly exist in the same flower, namely, the epicalyx, calyx, corolla, accessory corolla, the stamens, accessory stamens, and the carpels; yet I know no flower in which all occur in conjunction. All these foliar organs may be present in one or more circles, with the exception of the epicalyx, in which I know no example of a double circle. Perianth, calyx, corolla, accessory corolla, and carpels occur in one, or more rarely in two circles. Stamens may be present in one, two, three, or possibly even four circles; more *circles* than this are not exhibited in the normal condition of the flower. If the number is increased, which seldom happens, except in stamens and carpels, as in the *Ranunculaceæ* and *Dryadeæ*, the *Magnoliaceæ*, &c., they stand no longer in circles, but in a spiral. In Monocotyledons with perfect individualized flowers, with the single exception of some *Scitamineæ*, five trimerous circles of foliar organs of the flower appear to be formed in those where a second circle of petals exists. The greatest multiplicity of forms occurs in the Dicotyledons. *Lavatera*, for example, has an epicalyx, calyx, corolla, stamens, and carpels in five circles, with increasing numbers of members; those of the calyx and corolla alone are equal. *Gnidia virescens* has perianth, stamens, accessory stamens, and carpels, but in eight circles, which are throughout composed of two members each. It is by no means necessary that all the parts of a circle of floral foliar organs should be ultimately developed in the same manner; and many floral structures which have hitherto been apparently inexplicable may probably, by keeping this truth in mind, and following out the history of the development, be readily traced back to the original type.

The duration of the individual parts of the flower is very various; the axial organs, so far as they support the rudiment of the fruit, or aid in its formation, persist naturally, at least until the ripening of the seed, then fall away with it; or if it becomes disengaged from them, die away with the remainder of the plant. When axes bear only male organs or flowers, their duration is different; sometimes they are cast off at a true articulation, sometimes they remain upon the parent plant, and gradually die away. The

* Perhaps the Grasses and *Cyperaceæ* alone excepted, in which only one carpel exists.

foliar organs of the flower are equally various in their duration. Perianth, corolla, and accessory corolla commonly perish soon after the perfecting of the flower; either they are cast off by true disarticulation, or they wither upon the parent plant. The epicalyx and calyx frequently share the fate of the axial organs supporting the rudiments of the fruit; the carpels almost invariably. The carpels are rarely destroyed before the perfecting of the seed, as in *Leontice* and, according to Robert Brown, in *Peliosanthes Theta.* The stamens die away mostly immediately after the dispersion of the pollen; either they are cast off, or they dry up and die away within the flower.

The terminology in use is as follows: those parts which fail away immediately, when their perfect formation is but scarcely completed, are termed caducous or fugacious (*partes caducæ*); those which endure somewhat longer are termed, if they are cast off by disarticulation, deciduous (*partes deciduæ*); if they retain their position and die by gradual withering and drying up, marcescent (*partes marcescentes*); those parts which remain long, still vegetating, are termed persistent (*partes persistentes*); if they change their forms by further growth, they are termed excrescent (*partes excrescentes*).

In what has just been said there are three points to which I must draw especial attention, because they have most important influence on the mode of observation of the entire flower. They are by no means new facts, but their importance has not hitherto been properly recognised.

*a.* The first relates to the position of the parts of the flower. I will not enter here into the very acute theories of Schimper, but confine myself singly to the true observation of Nature. She gives us two distinctly separate conditions; namely, the origin of the foliar organs of the individual members in closed circles, in which all the individual parts appear simultaneously and at the same elevation upon the axis.* Where this condition obtains, the individual parts of the several circles alternate with each other, without one established exception that I know of; and where this does not occur in the perfect flower, an intermediate circle has always failed to develope, or parts have been esteemed independent which are not so in fact, as in *Potamogeton*, where the stamens are said to be opposite to the leaves of the perianth; but the so-styled perigonial leaves are only crest-like expansions of the connectives of the anthers, and not independent foliar organs. Probably exactly the same condition occurs in the *Proteaceæ*, an account of the development of which I have been unable to obtain. But I must observe that many of my investigations do not lead in the same direction. I may not pass over here the condition that in few- (two-) membered circles, as in the *Thymelaceæ*, every two-and-two circles approach together, and alternate in pairs, although observation proves that here originally four-membered circles are by no means present. All these plants belong to those which in descriptive botany are spoken of as definite parts (*partes definitæ*); and it is easy, by means of the equal number of members of a

* Examples of this are furnished by all *Liliaceæ*, *Irideæ*, *Palmæ*, Grasses with 3-merous; the *Labiatæ*, *Boragineæ*, *Compositæ*, *Campanulaceæ*, with 5-merous; many *Scrophulariniæ* with 4-merous; the *Berberideæ* with 3-merous; and the *Thymeleaceæ* with 2-merous circles.

circle that belong to one and the same part of the flower, as, for instance, the stamens, to reckon up the amount even for the greater number.

Close to those just named comes another condition, though far more rarely; where, namely the individual parts of the flower, either through the entire flower* or from the stamens forward, as in the *Ranunculaceæ*, or the carpels, as in the *Dryadeæ*, arise, one after another, in a spiral around an axis then mostly very much developed, and thus become perfected in succession. Here it is never specifically determinate, but only individually, with which members of the spiral, another form of the foliar organ shall enter, — for instance, the stamens be converted into carpels; — nor what shall be the greater number of foliar organs contained in the spiral; consequently, shall complete the entire flower. The plants here referred to are properly characterised as possessing indefinite parts (*partibus indefinitis*). In this way the said expressions of descriptive botany, which had been selected through a distinctly-felt necessity, and by a practical perception of nature, acquire, through the investigation of development, a rigid, scientific meaning which they really did not possess before, since no one could rightly say what *partes definitæ* and *indefinitæ* actually were.

*b.* The second point to which I desire to draw attention is the varied development of the members of one and the same circle, in which they assume forms such, that we are tempted to separate them entirely from the circles to which they belong; where, for instance, in the corollary circles some leaves become, if we may so say it, stamens; and in the staminal circles some become petals, accessory petals, or accessory stamens; or, in the carpellary circles, some become stamens, and some accessory stamens. One of the most striking examples of this is offered by the fourth and innermost tri-merous circle of *Canna* (fig. 195.). Properly all three parts should become carpels, and form the style; but one alone is folded in to form the style; a second becomes the stamen; and the third is wholly abortive, but exists in the tolerably large bud on a small scale, not very easy to represent. (See Plate III. fig. 12., with the explanation.)

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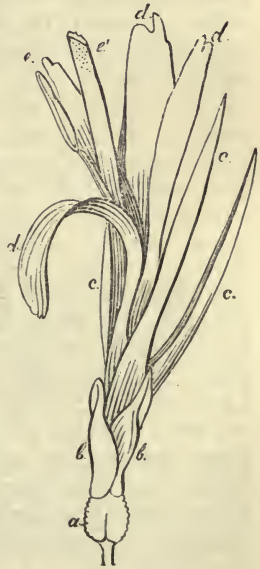


Many of the *Orchidaceæ* furnish known examples of the same fact, in which only one or two leaves of the innermost circle but one become stamens; whilst one or two, if they are not totally abortive, develope merely into small scales or glands. I may add, that something similar occurs in the generality of the *Scitamineæ*, but I have not had opportunity to follow out fully the history of the development. The *Balsamineæ* may, perhaps, be explicable in the same way, but I have not yet succeeded in detecting their earliest conditions with sufficient clearness. When the entire bud has reached only the length of from one-eighth to one-sixth of a line, the flower already has its contour almost as irregular as subsequently.

* Although I cannot bring forward any certain example of this, probably in the species of *Magnolia* and some *Ranunculaceæ*, especially the *Anemoneæ*.

195 *Canna exigua*, developed flower. *a*, Inferior germen; *b*, calyx; *c*, external, and *d*, inner circle of the corolla; *e*, stamens; *e'*, style.

The *Polygalaceæ* are also referable here, although I have not yet succeeded in finding out the earliest structure of the flower. The earliest condition of the bud which I have yet been able to arrive at, exhibits five free foliar organs in one circle, and within that, apparently placed in another circle, five other leaves, at that time also entirely free; of these the undermost becomes the pitcher-shaped, fringed petal; the two uppermost the bilobed petals; the two remaining side leaves are four-lobed; and each of these lobes is a perfect anther. The question remains to be solved whether this entire inner circle in truth originated as a pentamerous circle, whose two side members each represent a four-lobed stamen, since there is no other way of reducing the flower to regularity; or whether abortion had already occurred at a very early period.

*c.* The third point to which I wish particularly to draw attention is, that all foliar organs of the flower, though they may subsequently unite in growth, first arise entirely free parts; and if they belong to one circle, they are, at their earliest rudiments, and for some longer or shorter time after, exactly like each other; so that the coherence of these several members, and their symmetrical development, is a later process. I have been able readily to trace the most irregular flowers up to the condition of bud in reference to this; as, for instance, the flowers of the *Leguminosæ*, of the *Labiatæ*, the *Scrophulariaceæ*, and the species of *Aconitum*, and these fully established the laws laid down here. One of the most remarkable instances in this respect occurred in the stem of an *Orobanche*, which had not yet risen above ground, and which I came upon by happy chance, in digging for another plant. This exhibited such surprising regularity in tetra-merous circles distinctly alternating with each other, that nothing could appear more elegant. I have not yet succeeded in following out the perfect history of the development of the very irregular flowers.

I refer again to the flower of the Grasses (see Plate III. figs. 21—23., with the explanation, of *Agrostis alba*), and the *Carices* (see Plate III. figs. 24—26., with the explanation, of *Carex lagopodioides*.)

## C. Of the true foliar Organs of the Flower.

### a. *Of the floral Envelopes.*

§ 148. As among the floral envelopes are usually reckoned the perianth, the calyx, and the corolla, I also include the epicalyx here, and I circumscribe the term perianth in the narrowest sense, so that under it only those foliar organs fall, which, at least two in number, are applied closely to the flower, and upon one level; so that all individual foliar organs on the axis of the flower, which only enclose stamens or germens, are to be termed bracts. All these bracts have this in common, that they are merely foliar organs peculiarly modified; and, consequently, all the peculiarities of form which occur in the latter naturally appear in the former also. The few distinctions depend upon what here follows: —

As for all other foliar organs, so also for these all forms are

possible; but it is not often that the leaves of the floral envelopes have great thickness; they are almost always more or less flat. But the forms analogous to the pitchers or pouches are here frequent, much more so than is the case with the stem-leaves; and these are termed, according to their various resemblances to objects, cup-shaped, as the lower petal of *Polygala;* hood-like, as in the upper leaf of the perianth of *Aconitum;* and so on. If a long sac-like appendage * is formed at the basis of a perianthial leaf expanded above, the unhappily-chosen term spur (*calcar*) is applied, as in *Orchis, Delphinium, Fumaria,* &c. The formation of the spur is frequently conjoined with the formation of a symmetrical flower, where one upper or lower foliar organ forms a spur. The flattened, expanded form, which is connected with the axis by a linear prolongation, frequently occurs in the sepals (?). This expanded surface is termed the limb or blade of the leaf (*lamina*); the narrowed base is not termed petiole but claw (*unguis*). True articulation is frequent between the floral envelopes and the axis, but it never occurs in the continuity of these leaves (?); therefore there are no true compound perianthial leaves, though a simply divided limb is frequent, as the *petala palmatifida* in *Reseda,* the *petala pinnatifida* in *Schizopetalum,* &c. An indication of true articulation may probably be afforded in the separation of the upper part of the tube of the flower in *Mirabilis,* of the calyx of the *Datura,* from the lower, and in some similar cases.

True stipules are not met with in the floral envelopes, but appendages analogous to the *ligula* appear, to which, indeed, a part of the structure described as the *corona* belongs. As in the *Narcissus* and the *Lychnis,* the scales of the throat of the *Boragineæ* also belong here. These parts are formed in very various fashions on the floral envelopes, and such appendages are sometimes exhibited standing upon the surface of the foliar organ, in three or more rows, one above another. Almost all forms which descriptive botany recognises as *corona* and accessory corolla (*paracorolla*) belong here, in particular a part of those elegant forms exhibited in the *Stapeliæ* and the *Passifloreæ;* so also do a portion of the so-termed *nectaria,* as, for example, in the petals of *Ranunculus.* All these are mere dependant appendages of the foliar organs, which are developed originally simple and flat, all these parts being produced from them subsequently. Coherence and abortion have been already treated of. Here, also, occurs the one-sided development of a foliar organ: this is seen frequently in the petals of the *Apocynaceæ* (*Vinca, Nerium,* and *Cerbera*).

The collective form of one or more circles, whether coherent with each other or not, is more accurately designated according to further peculiarities, as tubular (*tubulosum*), bell-shaped (*campanulatum*), funnel-shaped (*infundibuliforme*), salver-shaped (*hypocrateriforme*), rotate (*rotatum*), &c.

* Exactly analogous to the pouch or pitcher in *Dischidia Rafflesiana* and *clavata.*

More will be said respecting this structure when we come to speak of the different kinds of floral envelopes.

Merely a few points require special notice here, because the principal facts are self-evident, as mere analogical application of what has been explained of the foliar organ in general.

In the first place, some further remarks are necessary on the distinction between perianth and involucre. Both are undoubtedly foliar organs on the axis itself; each foliar organ may be adherent at its borders or free; both may be green, brightly coloured, tough or delicate, like all foliar organs. The bracts may stand at various distances from the so-called parts of the flower; consequently, there is no distinction to be made between a one-leaved perianth and a bract, if we do not pay attention to the number of foliar organs arising on a level (in one circle) on the floral axis. Thus, and so alone, we acquire a perfectly strict and easily-maintained distinction for scientific description, if we only reckon anything as belonging to the floral envelopes when it consists of at least two foliar organs situated on a level, and call every other merely single foliar organ of the flower a bract. In this way we have a *bracteola urceolata* in *Humulus* and *Cannabis*, whereby in each case they are not so far removed, according to the usual mode of judging, from the true *Urticaceæ*, from which they are not to be separated at all, as when a *perianthium* is ascribed to them. The distinction between *Salicaceæ* and *Cupuliferæ* is easily described; although these plants are of very simple structure, they exhibit a manifest advance in the perfection of the flower. In the *Salicaceæ* the flower possesses no foliar organs; the *glandula hypogyna* in *Salix*, the so-called perianthium of *Populus*, are, according to their development, merely discs (axial organs). In the *Cupuliferæ* a perfect superior perianth exists; I have not yet become acquainted with the development of the *Betulaceæ*. This much is certain, the axils of the bracteal scales of the catkin do not bear single flowers but inflorescences (*capitula*), which distinguishes them widely from the *Salicaceæ;* but observation of the development can alone decide as to the import of the foliar organs which exist here. In the female flowers they are apparently bracts (not bracteoles), in the male of *Betula* the same, but in *Alnus* perianthial leaves. In the *Myricaceæ* and *Casuarinaceæ* distinct di-merous circles of floral envelopes occur. The *Piperaceæ*, including *Saururus* *, have the so-called naked flowers (without any envelopes) in the axils of bracts. Among the Monocotyledons the *Orontiaceæ* have a distinct perianth. Among the *Naiadeæ*, *Aponogeton* and *Ouvirandra* have some coloured organs on the flower, the nature of which cannot be determined for want of investigation of development; the scales of *Potamogeton* are nothing more than a scale-like crest on the connective of the anther. None of the others have any envelopes; in *Zarnichellia* the female flowers are enclosed by a single delicate bract † (*spatha hyalina*).

* The *Sauruaceæ*, as I have elsewhere observed, are not a distinct family, but a strange mixture of Monocotyledonous and Dicotyledonous plants, which has originated from imperfect knowledge; *Aponogeton* and *Ouvirandra* are true *Naiadæ; Saururus* is only generically distinct from *Piper* and *Peperomia; Houttuynia* I do not know, therefore I cannot say whether it alone will justify the establishment of a special family.

† The same botanists, who would of course admit that we can only speak of an hermaphrodite flower when stamens *and* germens are inclosed in one and the same set of envelopes, write coolly,—*Zarnichellia: flos hermaphroditus; stamen unicum stipulæ oppositum, germina quatuor perianthio inclusa.*—See Nees ab Esenbeck, *Genera Plantarum Flor. Germaniæ.*

It is indeed striking that (if my ignorance is not to blame) we have no example of a compound leaf in the floral envelopes, not even in such a way that a single articulation exists, as in *Citrus*, in the continuity of the same leaf. On the other hand, forms which are relatively rare in the stem-leaves occur here very frequently; for instance, the hollow ones.

A different and here especially attractive interest attaches to the distinct separation from the really independent foliar organs, of parts, which, though they appear in such striking and odd forms, are but appendages, and therefore portions of other organs. The terms corona, accessory corolla, nectary, &c., have hitherto been applied by botanists to the most different parts, with a truly inexcusable superficiality; and how little is dreamt in general of a scientific treatment of the matter, is seen in an expression of Link (*l. c.* ii. 145.), where he says of the accessory corolla of the *Passifloreacæ*, "We have no double forms by means of which to determine the true nature of this part." A simple examination of the young buds suffices to show that the various filaments and other appendages become developed out from already perfectly-formed foliar organs, consequently the former cannot be independent organs (see Pl. IV., with the explanation). Double forms, through which Link, for instance, decides upon the nature of the corona in *Narcissus* (196, *h.*), give *no results whatever*, since the double form is always

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[196] *Narcissus lætus.* Flower. *a*, Peduncle; *b*, spathe; *c*, bud; *d*, pedicel; *e*, inferior germen; *f*, tube of the perianth; *g*, limb of the perianth, appearing like six free leaves; *h*, corona, formed of six coherent ligules of the perianthial leaves.

a monstrosity, an aberration from the normal course of development; and there exists no principle here, by which to judge how far the plant deviates from its type to produce new forms, or how far the usual form is to be carried back to simpler elements. Assuming that the *corona* of *Narcissus* consists of independent foliar organs blended with the leaves of the perianth, may not they be multiplied in the doubling of the flower as well as the others, and, since their adherence to the perianthial leaves is merely a characteristic of the special nature of the flower, be isolated from each other and become blended one to each perianthial leaf? Monstrosities prove nothing at all here, but merely render probable; the only perfectly sure decision is to be obtained here, as everywhere, by tracing the development. In the paragraphs I have connected all these appendages to the analogy with the ligule, which is certainly warranted by the development for some forms, e. g. *Narcissus*, *Silene*, &c. In others, indeed, no such analogy exists, as in the *Passifloraceæ;* in very many forms we have no accurate investigations whatever, as in *Parnassia* and in the *Stapeliæ*. The fleshy portions of the latter form the transition to the thick fleshy *papillæ*, such as occur, for instance, in such strange forms in the labellum of the *Orchidaceæ* (*Oncidium*); on the other hand, the filiform appendages of *Passiflora*, which indeed belong partly to the disc, are more nearly allied to those tufts of hair occurring in more definite places, and with more definite colour and form, which are called beards (*barba*), for instance, on three of the perianthial leaves of *Iris*.

Finally, I will observe, that I have referred to the terms employed to describe the total form of the floral envelopes, as of general application, although most of them are only mentioned in isolated special cases, without involving any thing at all specific for one or other kind of floral envelope. Most of the words are very readily understood, some more difficult; e. g. *hypocrateriforme*, which will not be easily understood by any one who has not seen in old collections or old paintings the form of a flat plate supported on a long stem, on which wine-glasses were placed in the middle ages; floral envelopes are called rotate when they expand the separate organs equally or almost equally from the point of attachment in *one* plane. It also appears to me to be a mistake when a part of these expressions are applied solely to floral envelopes when the leaves are coherent, which merely gives rise to the necessity of imagining a new word for the condition with free leaves. What it is here required to name is the general contour, and therefore it is no more necessary to regard the subordinate divisions in these, than in the subdivided flat organs, such as the lobed and pinnatifid leaves. In rotate, salver-shaped, &c. corollas, however, the limb is always divided, which never is the case in a wheel or salver; and in this mode of naming we cannot convey ideas of degrees of more or less, so that in the corolla of *Lychnis* and *Dianthus* the words *corolla* (*pentapetala*) *hypocrateriformis* answer the purpose very well.

§ 149. Five kinds of floral envelopes are distinguished. When all the foliar organs are similarly or nearly similarly developed in a circle of one evident form, colour, and structure, they are described under the general name of *perianth*, the single organs of which are called *perianthial leaves*. If in the floral envelopes of one flower we can distinguish two circles differing in form, colour,

and structure, the outer is named the *calyx*, its component organs being *sepals;* while the inner is termed the *corolla*, its single parts *petals*. Then, if three circles of forms are distinguishable, the outermost is called the *epicalyx*, the leaves of which may be denominated *phylla*. When, between the simple or manifold floral envelopes and the stamens, other independent foliar organs occur, which exhibit a structure very imperfect and abnormal compared with the true envelopes, these are called a *paracorolla*, of which it will be necessary to speak further on, among the accessory parts of the flower.

It would be vain to seek in most of our botanical works for an explanation of what really is the distinction between the separate kinds of floral envelopes. Here, as almost everywhere else, botanists are careless about scientific treatment, about strictly defined conceptions. The individual forms are taken up diagrammatically, the internal unity not perceived, because no correct method is used, and thence the accurate comprehension of the external distinctions in the phenomena also becomes impossible. How childish are the many contests we have had as to whether a plant had a calyx, a corolla, or a perianth; people had forgotten that for the decision of this point it was first necessary to examine whether nature does generally exhibit these three kinds of foliar organs as different, and if so, how nature (not we with our fancies) distinguishes the parts. In nature we find the distinction so, and in no other manner, as I have given it in the paragraph, since all floral envelopes consist of foliar organs, in which a countless multitude of varieties of form, colour, and structure are equally possible. Where all the parts are developed alike, they are consequently only like parts, to be named with one word, undoubtedly the simplest and most natural condition; where, on the other hand, differences manifest themselves, the subdivision thus produced may be distinguished by the application of different names, which at the same time are only valid when the differences actually exist, and none of which are ever to be used where nature herself has not made a distinction. It is therefore a fundamental error when Kunth (Handb. der Botanik, 81.) carries over the term calyx to the perianth, since it is not the calyx, but calyx and corolla together; which correspond to the perianth, and it is an empty, groundless fiction to say that when only one set of similar envelopes exists, the corolla is always wanting. Lindley (Introduction to Botany, 11th ed. 136.) has comprehended the conditions most correctly and clearly on the whole, but errs when he speaks of calyx and corolla in the *Liliaceæ;* here nothing is to be founded on the number of circles, otherwise the *Thymelaceæ* would also have calyx and corolla, and a new word would be required for the *Berberaceæ*, since these have four circles of floral envelopes. How far very many botanists still are from having, I will not say a deep insight into the nature of plants, but merely a conception of the primary principles of the true study of nature, is shown by a remarkable expression of Ach. Richard. He says: "The floral envelopes are . . . . . somewhat modified leaves. . . . . It is often difficult not to regard them as one and the same organ. Meanwhile botanists *have agreed*, in order to facilitate the establishment of the generic characters of plants, to regard them, in consideration of their position and purpose, as altogether different from the organs with which they at the

same time agree in internal structure." Such a convention among botanists, did it actually exist, would be a foolish agreement to obscure nature instead of comprehending her better. As I have before said, we do not make the forms with our ideas, but receive them from nature; and our object is to learn to understand nature, to divide where she divides, and to leave united what she herself does not distinguish. If, then, nature herself exhibits to us a certain complication of foliar organs united into one general form, and thus separating themselves from the other foliar organs, on this account, and not in consequence of a convention altogether valueless for the perception of nature, do we distinguish the floral envelopes as special organs. On that point, however, whereon the concurrence of botanists has to decide, namely, what word shall be applied to denominate the organ distinguished by nature, they have not, unfortunately, come to an agreement, just from the fact that they are altogether destitute of the correct principle of investigation. That nature gives us flowers in definite general form, in the *Phanerogamia*, is certain; and just as certain is it that these flowers frequently consist externally of one or more circles of foliar organs not essentially altered; that when many of these foliar organs are present, these are developed either similarly or dissimilarly; that they are sometimes all green, sometimes all bright-coloured, sometimes partly green, sometimes partly bright-coloured: which are all facts, not derived from us, but from nature. When these variations have to be named, and this is in general an arbitrary matter, the certainty of scientific language requires an *universal* agreement, from which variety and the desire of novelty of the individual, cannot detach itself without stepping as a direct stumbling-block into the path of science. These terms must not be so chosen that like things have different names, different things like names. If the outer circle of different foliar organs is called a calyx, several circles of similar organs must not receive the same name. The first thing is to find out what forms nature gives us; the second is to give these names; and here scientific language demands, for its safety, the most rigid logical consequence.

What Ach. Richard says about the floral envelopes of Monocotyledons is scarcely grounded on even the most superficial observation, but rather a pure arbitrary invention, to support his equally arbitrary subdivision of the floral envelopes. He says, "Although the six segments of the floral envelopes of the Monocotyledons stand in two rows, yet they form only a single circle on the summit of the pedicel which bears them; that is, they have only one common point of origin on the receptacle, and evidently all six develope from the *outer* parts of the pedicel." In these last words it is evident that Linnæus's fancy of the import of the bark, liber, wood, and pith, in the origin of the parts of the flower, was in view, and yet with ridiculous want of consistency; since Richard himself explains *all* floral envelopes, therefore also the corolla, as foliar organs, and *all* foliar organs arise *on the* stem in the very same way, and not some from the outer and others from the inner parts. I will not refer to the course of development here, which at once shows how groundless Richard's assertion is; it is sufficient to call to recollection a *Commelina* or a *Tradescantia*, where three and three floral envelopes originate as evidently at different heights upon the receptacle as can be the case in any calyx and corolla of a Dicotyledonous plant.

What causes the greatest difficulty in the accurate and certain application of names is what has to be understood as similar and dissimilar.

Here, as in all cases where a purely empirical matter is in question, it is infinitely difficult to express in words what a single glance at nature establishes with facility. In point of fact, nature is not indeed so changeable and undefined as might appear at the first glance, for it is our imperfect perception that produces the indeterminateness in nature. With a complete and profound knowledge of all plants, it would be easy enough, even by a simple sign, without the application of our so uncertain terminological instrument, to characterise a given flower intuitively; but for this is required a knowledge of the laws of the structure of forms, of which we have not yet even a presentiment. For the present we must make use of various external aids, but select these in such a manner that they may put no compulsion upon nature, but leave the path open to progress in the science. This is only possible by a construction of the definition from *actual experience*, instead of out of a pretended theory which cannot exist at present; and, further, by rigid logical classification of the definitions according to their relative value and dependance upon each other. In the Phanerogamous plant we have, in this way, the axis and leaf as the primarily defined differences; *subordinate* to this division come the distinctions founded on progressive development and position, therefore on time and space, as the most universal; then we arrive at the conditions of form, structure, and colour, which are neither to be evolved from the nature of the plant at present, nor have any relation to primary intuitions, therefore can only be empirically comprehended through experience, and must be described with æsthetic clearness. Thus the conception of similarity admits of no general definition in regard to the floral envelopes, but requires actual demonstration; and here we are destitute of the comprehensive knowledge of all cases from which the more general or more restricted importance of the individual characters might with certainty be deduced. Here we must confine ourselves almost entirely to certain groups of plants, within the limits of which an example does not readily lead to error. If we take, for instance, a corolla only symmetrically developed, e. g. a Pea flower, a striking difference among the separate foliar organs cannot be denied; nevertheless they have a certain agreement in colour and texture, which determines us to recognise them as *similarly* developed. How, in most *Orchidaceæ*, the lip differs in form and colour from the rest of the perianthial leaves, and yet there is something in its texture in which we perceive it to be similar to them. Colour and texture agree almost perfectly in the calyx and corolla of *Ranunculus acris*, and yet we distinguish here two dissimilar structures, according to form. Structure, colour, and even almost form, are exceedingly similar in the floral envelopes of the *Amarantaceæ*, and nevertheless we separate, directly we see them, the corolla from the calyx (the inner two of the three so-called bracteoles), &c. From these causes we can, in General Botany, in regard to very many conditions, only indicate the directions in which the study of these has advanced; and instruction in these things must be given by pointing them out in actual specimens; more special explanations are only possible in Special Botany, in reference to particular groups of plants, and the attempt to gather them into generalities leads to endless complexity and useless time-wasting repetitions.

I have included the epicalyx among the floral envelopes; and, true to the fundamental axiom, that what nature unites man may not divide, I also

reckon among these the outermost circle of leaves, closely applied to the flower, and so gathered together as to form a collective object in the flowers of *Dipsaceæ*, in many *Malvaceæ*, *Passifloraceæ*, &c. Many persons, in defiance of all correct modes of naming, call these *involucrum* or *involucellum* in the Dicotyledons, *spatha* in the Monocotyledons — terms which were originally applied to bracts, or a circle of bracts surrounding an *inflorescence*, and are in the highest degree unsuitable; and even include here parts which cannot be called anything but calyx without a complete confusion of terminology — as, for instance, the outermost circle of floral envelopes in *Scitamineæ*, &c. The only parts which can be confounded with the epicalyx, and to which it naturally forms the transition, are bracteoles upon the pedicel; but of course, where nature has not united them in definite form and arrangement to the flower, as in the plants mentioned, no epicalyx exists, but merely bracteoles. It is indeed very difficult to draw a line here, as in the distinction between *flos pedicellatus* and *flos sessilis*, since it is not an absolute difference, but merely a question of more or less that has to be decided on. It is again a point, where the more refined cultivation of the perceptive faculty, where the tact of the inquirer can alone give a correct determination, if we do not agree to arbitrary absolute measurement, which would be exceedingly useless, since in difference of size of flowers that very absolute measure, for instance a line, becomes relative. In some flowers, as in *Parietaria*, a line is an enormous deal; in others, such as *Datura* or *Brugmansia*, &c., nothing at all. Where, as in *Passiflora*, elongated internodes occur within the undoubted flower, it would be the readiest expedient to measure; but this is rarely the case, and therefore this best expedient admits of only limited application. On the whole, a doubtful case will rarely occur, if a man endeavour, with a genuine and refined feeling for truth, to understand nature, and not try to adapt this to his own preconceived opinions.

The epicalyx, as I define it, may co-exist both with a true calyx and with the perianth, but, in the latter case, only where it is separated from the perianth by the inferior germen, since otherwise there is no cause why it should not be called the calyx, as, for instance, in the *Amarantaceæ*.*

The paracorolla may also exist in the perianth, but it is always sufficiently characterised by the aberrant structure of its foliaceous portions, so that it cannot be confounded with the corolla, and the perianth taken for a calyx.

§ 150. The perianth consists, according to the preceding considerations, of one or more circles of leaves, which are developed so as to be similar in colour, form, and structure. The following series of its forms may be more minutely characterised.

The individual foliar organs are always (?) expanded in a flattened form, seldom divided into limb and claw, and, at least when

* In almost all descriptions of the *Amarantaceæ*, one reads *flores tribracteati*. That one of these leaves belongs to a totally different axis, namely, the peduncle, is wholly ignored here. In the *Polycnemeæ*, however, where exactly identical parts exist, and only one leaf, namely, the only true bract, is green, we find, *flores quia in axilla folii sessiles bibracteati*. If an Amarantaceous plant should occur with coloured bract and green calyx, it would probably run, *flores quia in axillis foliorum duorum sessiles unibracteati ! !* How shall we describe this sort of thing adequately ?

they are not coherent, usually oval or lanceolate. They may be green, as in the male flower of the *Urticaceæ*, or of various colours, as in *Thymelaceæ;* they may be firm and solid, and that especially when green, as in *Elæagnaceæ;* or of delicate texture, as in *Aristolochiaceæ;* or they may be developed as delicate sapless scales (*paleæ*), or bristles and hair, as in the *Typhaceæ* and *Cyperaceæ*. The perianth is almost universally regular, rarely (in some *Ranunculaceæ* and *Orchidaceæ*) symmetrical; in these cases never (?) two-lipped, but often with one lip, as in the *Orchidaceæ*. This is then not infrequently developed hollow (*cucullatum* in *Aconitum*, *calcaratum* in *Orchidaceæ*), and it is commonly the uppermost leaf of the perianth. Its foliaceous portions may be free, as in *Juncaceæ;* or coherent, as in *Funkia*, *Hemerocallis*, &c.; they may consist of one circle, as in *Urticaceæ*, or of more, as in *Liliaceæ*. The parts are frequently blended with the stamens: in the coherent perianth the tube is sometimes straight, as in *Narcissus;* sometimes curved, as in *Aristolochia*. The mouth is mostly naked; sometimes, but seldom, as is the case in *Narcissus*, furnished with appendages which form a corona, which, however, are rare in the perianth, and in free foliar organs only (?) occur on the lip: the inner circle often has a beard.

According to the definition that has been given of the perianth (196.), it cannot be questioned that in some families, as, for instance, the *Rosaceæ* (in its widest sense) and in the *Ranunculaceæ* (fig. 197), we may sometimes have a perianth, and sometimes calyx and corolla. But when the matter is correctly considered, this is of no importance, since the unity of the type depends not upon the names we give things, which are merely to express our experiences, but upon the general structure of the plants, which ever is and must be subject to a multitude of specific modifications and changes. Floral envelopes are only foliar organs, and the character of any particular group of plants seldom rests only upon their peculiar formation. The attentive observer of nature easily traces the relation in certain vegetable groups, but this relation is unaffected by the terms with which we may choose to characterise the groups briefly; and on account of our deficient knowledge of the vegetable world, it is most difficult always to apply the correct expressions. The history of the development can alone help us here, for the unity of the group always lies in certain forms of the process of development; and here we are scarcely on the threshold of our science.

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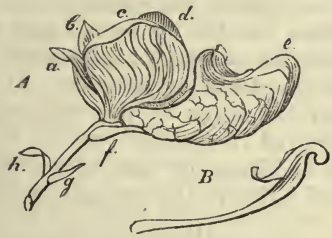


[197] *Aconitum napellus.* *A*, Flower: *a* to *e*, five perianthial leaves; *e*, hood-shaped; *f*, *g*, *h*, three bracteoles. *B*, Leaf of the accessory corolla.

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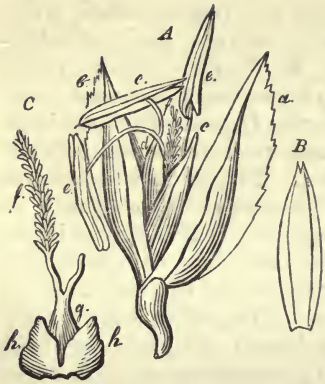


The perianth of the female flower of *Carex* is peculiar; it is originally three-leaved, but one leaf very soon ceases to grow, whilst the others, developing disproportionately, unite by their edges and enclose the stunted leaf, and thus form the tubular envelope of the germen, which has been termed *utriculus*, *cupula*, &c. (See Plate III., figs, 24. 26., with the explanation.) The perianth of the Grasses is similar (fig. 198.); it originally consists of three leaves, of which one (*palea exterior*) is excessively developed, and encloses the other two, which soon cohere and grow imperfectly into a membranous structure (*palea superior binervis*. (Plate III., fig. 21—23., and explanation.)

The structure of perianthial leaves is, on the whole, that of very simple leaves, which exhibit no special peculiarities, particularly if they are green. The ramifications of the vascular bundles are therefore simple, the separation into an upper and under parenchyma layer is seldom exhibited; but the epidermis usually. In the coloured and delicate parts the cells of the parenchyma contain colouring matter. In general the parenchyma is very loose and almost spongy, with homogeneous, transparent fluid contents, and large intercellular cavities filled with air; hence the white colour. The epidermis is less developed in coloured leaves, and more resembles the structure of epithelium; stomata are sometimes present, especially upon the under surface, but the epidermal cells of the upper surface are often raised in shorter or longer papillæ, which give the upper surface the peculiar velvet-like appearance. It is very frequent here to find the secreted layer of the epidermis (cuticle) regularly and delicately striated (*aciculatus*), which certainly contributes to heighten the brilliancy of the colour, and perhaps, by its effect upon the rays of light, to the production and modification of the peculiar tints.

Occasionally, especially at the base of hollow forms, no epidermis is produced at certain points, and the parenchyma assumes a peculiar structure, to perform the function of secretion of a juice containing much sugar; as, for instance, the nectary at the base of the perianthial leaves of *Fritillaria*, very various parts on the *labellum* of the *Orchidaceæ*, &c. In rare cases the texture is hard and almost

[198] *Phalaris cœrulescens*. *A*, Spikelet: *a* and *b*, spathe, formed of two bracteæ (*valvæ glumæ*, Auct.); *c* and *d*, one free and two coherent perianthial leaves (*paleæ*, Auct.); *e e e*, three stamens; *f*, a stigma. *B*, The two coherent perianthial leaves, with two nerves (*palea superior*, Auct.). *C*, Pistil, surrounded at the base by two weakly coherent accessory petals: *h h*, (*squamulæ*, Auct.); *g*, germen; *f*, one stigma; the other is cut off.

woody from the interspersion of many thickened, porous parenchyma cells, as in the species of *Banksia* and *Dryandra* (?). In paleaceous perianths, the spiral and other vessels are not found in the usually simple vascular bundles, and in hair-like perianths even the vascular bundles themselves are wanting.

§ 151. The calyx only exists when a corolla occurs with it; it therefore can never be confounded with it. It is always the external of two dissimilar sets of envelopes. Its series of forms very much resemble those of the perianth; perhaps it is not so frequently delicate in structure and colour (as in the *Scitamineæ, Musaceæ, Butomaceæ, Ranunculus, Tropæolum*, &c.). Usually it consists of one circle of sepals, more rarely of two (as in the *Berberidaceæ*). These sepals are always very simple, oval, or lanceolate, seldom pinnatifid, very frequently broad at the base and tapering to a point, or *very* small (*dentes calycis obsoleti*); sometimes they appear only as dry scales, or as tufts of hair (the *pappus* of the *Compositæ*). Appendages seldom occur upon the sepals, but they are frequently of hollow or concave form. The number of the sepals in each circle is in Monocotyledons frequently three, more rarely four or two; in the Dicotyledons it is most frequently five, but also two, three, or four (and, perhaps, sometimes more). Coherence of the sepals with one another may occur in every way, but, so far as my knowledge extends, never with the corolla and stamens, nor with the germens; that which is so called being quite an other condition (which has been already explained (§ 146.) as the inferior germen). Both in free and in coherent sepals, regularity and symmetry are met with, the latter often exhibit the bilabiate structures.

That which has been said of the structure of the perianth applies also to the calyx, only that here green foliar sepals are the more frequent.

The definition of the calyx, rightly comprehended, presents no difficulty whatever, and it is only necessary to give a few examples to guide in observation. For this purpose we select the three-leaved calyx of *Canna exigua* (fig. 195.), the four-leaved calyx of *Isatis tinctoria* (fig. 199.), the coherent form of *Salvia patula* (fig. 200.), and the undeveloped one (*pappus*) of *Actinomeris alternifolia* (fig. 201.). The development of the calyx, so far as it appears necessary, is exhibited in Plate IV. in *Passiflora princeps.*

§ 152. The corolla, which only exists as the inner set of floral envelopes accompanying a calyx, may be compared to a very delicate and coloured perianth. So far as my knowledge extends, no true corolla occurs perfectly green and resembling the leaves; its series of forms is greater than that of any other of the floral envelopes. In the Monocotyledons it presents in general only simple, round, oval, or lanceolate leaves, very seldom having claws. In the Dico-

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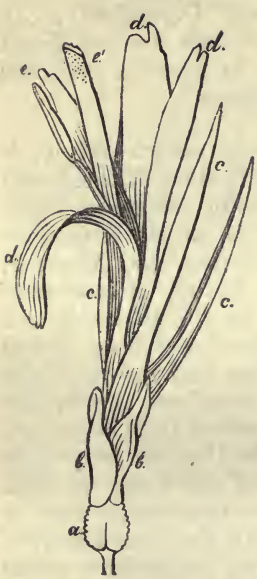


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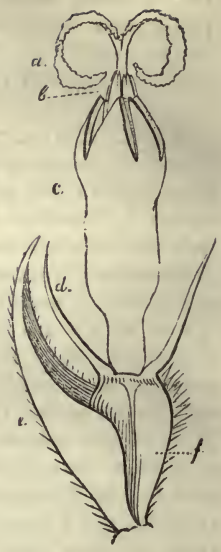


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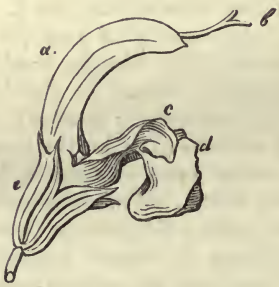



tyledons the forms are infinite, as are also the variety and splendour of the colour. The following are the main points: —

The individual petal exhibits, on a reduced scale and in a delicate condition, almost every variety of form of the leaf, with the exception of the truly compound. Concave forms are here frequent, such as the hood-shaped, pitcher-shaped, or spurred petals, &c.; these latter very often on individual petals of an otherwise regular corolla (as, for instance, in *Fumaria*). Fringed and feathered forms, as well as variously lobed petals, are also by no means rare. The limb and the claw are often clearly to be distinguished. Parts analogous to the ligule, and every imaginable form of appendage, with the exception only of the stipules, occur frequently, and characterise genera and families.

On this account it is indispensable to distinguish the simple appendages of the petals from the independent foliar organs. To the former belong the scales (*fornices*) of the *Boraginaceæ*, the scales of the corona of the *Sileneæ*, the formations generally

[199] *Canna exigua.* Developed flower. *a*, Inferior germen, *b*, calyx; *c*, external, and *d*, internal circle of the perianth; *e*, stamens; *e'*, style.

[200] *Isatis tinctoria.* Flower. *a*, Four-leaved calyx; *b*, four-leaved corolla; *c*, six stamens; *d*, pistil.

[201] *Salvia patula.* Flower. *e*, Five-membered coherent bilabiate calyx; *a*, upper lip of the 5-merous coherent bilabiate corolla, formed of two leaves; *c*, *d*, lower lip, formed of three leaves,—a central and two lateral ones; *b*, style and bifid stigma.

[202] *Actinomeris alternifolia.* Single flower. *e*, Bract (*palea*, Auct.); *f*, inferior germen; *d*, stunted calyx, originally five-membered (*hairy crown*, *pappus*, Auct.); *c*, tubular corolla, formed of five coherent petals; *b*, tube of the five cohering anthers; *a*, style with two stigmas.

described as coronæ in the *Stapeliæ* and some other *Asclepiadeceæ*, the nectaria of *Ranunculus, Parnassia*, &c.

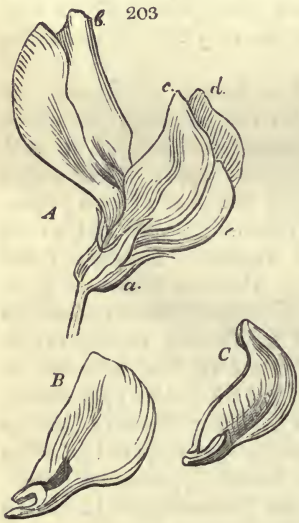
The corolla consists of one circle, rarely of two (three series in *Berberis*) or more (four series in *Nymphæa*). In Monocotyledons the number of members is equal to those of the calyx; in Dicotyledons, the number of five in a circle predominates, though it is sometimes composed of two, of four, or of greater number (in *Dryas*) (?). The number of members is equal to that of the calyx, or greater; very rarely indeed is it smaller; this last case occurs with *Hibiscus*. Suppression is not infrequent, and sometimes involves all the foliar organs of a corolla at once (for instance, in the summer flowers of many species of *Viola*, in *Lepidum ruderale*, and some species of *Acer*). The coherence of organs in every way is still more frequent; never, indeed, with the calyx or the germens, but frequently with the stamens.

The corolla, whether with free or with coherent petals, may be regular or only symmetrical. In the latter the bilabiate formation is the most frequent, especially in five-membered circles, in such a way that, according as the odd petal is on the upper or the under side of the flower, the upper lip consists of three or of two petals. In the latter case these two are very often little or not at all coherent, as in *Teucrium*, the so-called radiated flowers of the *Compositæ* (*floribus ligulatis vel radiatis*). Peculiar forms of symmetrical flowers are, for instance: the personate flowers (*corolla personata*), in which the upper petals of a coherent corolla are so curved inwards that they close the entrance of the tube (as in *Antirrhinum*): the incurved portion is termed the palate (*palatum*); the true bilabiate or mouth-like corolla (*corolla ringens*), in the *Labiatæ*, in which the two petals forming the upper lip often present a concave form overhanging the lower lip, termed *galea*; the so-called papilionaceous flowers of the *Leguminosæ*, in which the uppermost leaf, which is broad and large, surpassing the others, is termed the standard (*vexillum*), whilst the lateral petals, as wings (*alæ*), are usually dissimilarly developed, and the two undermost, very frequently coherent, also developed unequally at the two sides, approach each other in a concave form, so as to form the keel (*carina*). Sometimes all the petals of the papilionaceous flowers become coherent at the lower part, and form a tube, as in *Trifolium*; or individual petals are abortive, &c. The most irregular of all the forms have hitherto received no names; such as appear, for instance, in the *Polygalaceæ*, the *Balsaminaceæ*, *Tropæolaceæ*, &c.

All that has been said respecting the structure of the perianth holds good of the structure of the corolla, except that this is more delicate. The contents of the cells vary very much in colouring matter, and their distribution in groups is sometimes very remarkable. Very dense texture, in consequence of the presence of much-thickened porous cells, as in the *Amarantaceæ*, is infrequent.

The structure of the epidermis, and its development into papillæ, hairs, &c., is very manifold. Development into surfaces secreting nectar, both at the bottom of concavities and upon the appendages, is especially common. The petals also occasionally secrete a viscous substance, in consequence of which they adhere together, as happens at the points of the inner petals of the *Fumariaceæ*. I know of no other remarkable condition requiring notice.

I will here present merely a few examples of the forms described in the foregoing paragraphs, exhibiting the tetra-merous, cruciate corolla (fig. 200.), the bilabiate (fig. 201.), the tubular (fig. 202.), the papilionaceous (fig. 203.), and the many-leaved cup-shaped (fig. 204.). The development of the regular corolla of *Passiflora princeps* is given in Plate IV.



From the multiplicity of its forms and the variety of its colours, the corolla has in all times attracted attention, and so, from the earliest period of the scientific study of Botany, much, perhaps too much, relative stress has been laid upon the knowledge of it, whilst the other parts of the plant have been comparatively neglected. That, in the general destination of the vegetable world to favour pre-eminently brilliant and varied play of forms, and thus to become the richly decorated garment of the geologically naked and poverty-stricken earth, the organ especially devoted to the production of this wealth of form should express the essential character of individual groups, genera, and even species of plants, is of course to be expected; but it is still even only a part of a number of organs of equal importance, and in the scientific view of plants the corolla must be considered even as a subordinate part, because we are wholly ignorant of the laws of the production of form, and by giving it a partial pre-eminence we should deviate most widely from our aim. In General Botany there is particular necessity merely to indicate the points of view from which one has to observe the infinite abundance of specialities; and this I have endeavoured to do in the paragraphs. To go further into the structure of the corolla of particular groups I consider to be a mistake, and in the highest degree confusing to the

[203] *Lathyrus odoratus*. Flower. *A*, *a*, Penta-merous coherent calyx, surrounding a 5-merous irregular papilionaceous corolla; *b*, upper petal (standard, *vexillum*); *c*, *d*, and *B*, two lateral petals (wings, *alæ*); *e* and *C*, two lower petals, coherent at the lower border (together the keel, *carina*).

[204] *Malva miniata*. Flower. *a*, Three-leaved epicalyx; *b*, 5-merous coherent calyx; *c*, five-leaved corolla.

learner. The elucidation of these specialities belongs to Special Botany, where, however, the development of the characters of families must be carried out much farther than is done in the present barren summary of the equally barren descriptions of genera.

I have nothing more to add to what has been said in the paragraphs.

§ 153. The epicalyx is exhibited when three several series of foliar organs are distinguishable in the floral envelopes, and it is the outermost of these. There are not many plants which possess an epicalyx; still fewer are the families in which it is constantly presented. In form and structure it much resembles the calyx. It occurs with free leaves, as in *Passiflora;* and coherent leaves, as in *Lavatera.* Its leaves are seldom delicate like those of the corolla, but are often dry and membranous, as in *Scabiosa,* but generally green and leafy, as in the *Malvaceæ* and *Dryadeæ.*

Since all floral envelopes are but foliar organs peculiarly modified, and since the bracteoles situated on the floral axis below the flower may assume almost all those modifications, so naturally we cannot set a boundary to the flower below by means of the definition, where such a boundary is not presented to us by nature. In the families of the *Malvaceæ* (fig. 204.), *Dipsaceæ,* and *Passifloracæ,* certain circles of organs are united into a collective form outside the calyx, and evidently in a very close relation to the flower; and these therefore, no less than the calyx, deserve to be accepted and characterised as one special form of the floral envelopes. In all families with dispersed leaves, no doubt can exist as to the distinction between bracteoles and epicalyx, if the latter be described as *one* leaf circle close outside the calyx or spiral. In a verticillate arrangement of the leaves, the distinction might be more difficult; but I am not acquainted with any such case.

Some Botanists have imagined that they have cleverly explained the epicalyx of the *Dryadeæ,* as, for instance, it appears in *Potentilla,* where they have deduced it from the coherent stipules of the calicine leaves. Such false ideas and false explanations are the inevitable consequences of the perverse method of guessing instead of investigating. The epicalyx of *Potentilla* and its allies is a true leaf circle, and, as is self-evident, the first which is formed on the entire flower, and the sepals arise subsequently and higher upon the axis as the second circle of leaves.

### b. *Of the Stamens.*

§ 154. The stamen is doubtless a true foliar organ, and of all the foliar organs of the flower is that which exhibits forms the most analogous to the stem leaf.

It is the only foliar organ of the flower which is not merely defined morphologically by its form and position, but also physiologically determined by the importance of its peculiar structure to the formation of the spore, here called the pollen. The law here is: Where no pollen is formed, there is no stamen. The

terms *stamina abortiva* and *stamina castrata* have no meaning. In that relation it corresponds completely to the sporophyll of the cryptogamic stem plants, and the forms there exhibited as typical of classes are here again manifested to characterise families or genera.

We find here the sporophyll of most Ferns, developing a number of capsules (here termed cells, or *loculi*), out of the under face of the leaf, in the *Cycadaceæ*. In many Coniferous plants, only a few, long and tubular loculi are formed on the under surface (as in *Cunninghamia*). In *Juniperus*, *Cupressus*, &c., the stamens cannot be distinguished at all from the sporophyll of the *Equisetaceæ*; and we find in *Humirium* and *Glossarrhen*, where, however, two loculi are presented instead of one, an analogy with the sporophyll of the *Lycopodiaceæ*, where a capsule is formed on the upper surface of the base of a flat foliar organ. But the stamen usually corresponds to the sporophyll of the other Ferns, in which only the petiole and mid-nerve of the leaf are perfected, at the sides of which the parenchyma merely forms the loculi. The structure, however, corresponds not to the much divided Fern leaf, but usually to a simple flat leaf, with a petiole. Then it exhibits an attenuated basis (the petiole is here termed *filament*), and an upper broader part, the blade of the leaf (here termed *anthera*). In the anther, we further distinguish a middle part (the mid-nerve of the leaf, here termed the *connectivum*) from the lateral parts, the chambers (*loculi* or *thecæ*) which appear at the summit, the edges, the upper or under surface of the connective as globular, oval, or long cylindrical projections; besides these, the original edge of the leaf as a longitudinal furrow (*rima longitudinalis*). Finally, in many stamens the entire leaf substance, in analogy with the so-called sessile leaf, is applied to the formation of pollen-chambers (*anthera sessilis*).

Each stamen originates as a leaf, runs at first through a similar series of forms, and its subsequent peculiar appearance is merely a result of its special mode of development, which may be traced, not merely ideally, but mostly really, in the progressive development, to a few simple fundamental types. Besides the cryptogamic type, above followed out in the families of the *Cycadaceæ* and *Coniferæ*, a Phanerogamic type is also to be traced; which essentially consists in the circumstance, that, independently of the presence of the filament, a flat leaf is so developed that its mid-rib becomes the connective, its edge the longitudinal furrow, its parenchyma swells out on both sides of the connective, in which then, through the formation of the finally free pollen-grains, one (as in *Abies* and the *Asclepiadaceæ*) or commonly two thecæ are commonly formed on each side. This type doubtless lies at the base of all Phanerogamic stamens, if we except *Najas*, *Caulina*, and some *Araceæ* (of which I do not know the history of development). All further peculiarities concern either the development of the thecæ on one side alone

(as in *Canna* and *Salvia*), or the excessive development of the connective, either altogether, so that the thecæ are more or less removed from each other (as in *Lacistema* and *Salvia*), or at its base (as in *Stachys sylvatica*), at its upper part (as in *Berberis* and *Humirium*), or on the under surface, so that the thecæ have the appearance of lying upon the upper surface (*antheræ anticæ, introrsæ*), or on the superior surface, so that they have the appearance of lying upon the under surface (*antheræ posticæ, extrorsæ*); or several of these modes of excessive and disproportionate development may occur together. Further, we find very irregular development of the connective, and of the thecæ dependent upon it; for instance, in the serpentine form (in many of the *Cucurbitaceæ*), the thecæ rolled inwards like the Corinthian volute, in *Philydrum*, &c., all originally starting from the same structure, and only gradually assuming these forms. Besides the forms already mentioned, other irregular growths of the connective are presented, especially upon the under surface, where they assume strange forms of spurs, hoods, &c., as in *Asclepias*, &c.: all these varieties are generally thrown into a heap with things of the most different nature, under the name of *corona*. On the thecæ also occur, sometimes in the upper and sometimes in the under part, processes and appendages of very various kinds (as in the *Ericaceæ*). The connective expands in a very peculiar manner on the back of the anther, beyond it, but projecting especially above and below, and encasing it as a coat, as in many of the *Apocynaceæ*.

Many varieties occur in the mode of union of the anther with the filament; sometimes no filament is formed. When it exists, it sometimes again merges into the connective, which appears somewhat broader than it, and the base of which is not surpassed by the base of the loculi; or the latter grow further out beyond it, so that the filament seems to be inserted between the thecæ corresponding to the *folium cordatum* or *sagittatum;* or the thecæ are developed out in a similar manner beyond the base of the connective, and become blended in the course of their formation, corresponding to the *folium peltatum:* this is termed *anthera dorso affixa*, or, as it is usually unsteady upon the slender filament, *anthera versatilis*. Again, the filament corresponding to the petiole offers a multitude of varieties; sometimes it is linear or flat (band-like), or may be developed thick and fleshy, exhibiting all kinds of appendages both upon its upper and under side, and especially such as correspond to appendages on the leaves: thus, for example, like the ligule (in *Cuscuta* and some species of *Zygophyllum*); and in particular appendages corresponding to the stipules (as in many *Lauraceæ*, *Amarantaceæ*, and species of *Allium*, *Alyssum*, and *Campanula*), which is the more remarkable, since no other foliar organ of the flower exhibits anything similar.

A true articulation in the continuity of the same stamen I have nowhere found; in the *Compositæ* it is certain that no such thing

exists. Coherence of every kind occurs here; the stamens sometimes become blended in the entire length; or the filaments cohere in part or entirely; the filament with the perianth or the corolla. Coherence of their stipules also occurs, as in the *Amarantaceæ*.

We have here again a few points to bring forward, which require a more minute exposition, in order to establish an accurate comprehension of the stamen.

In the first place, I must discuss the proper definition of the stamen. In this matter I need spend no more words than are necessary to say that it is a modified leaf, since all Botanists whose opinion is of the slightest consequence are now agreed upon this point: but this does not do much for the formation of the definition; we have such a multitude of kinds of foliar organs, which comprehend the whole region of possibility of conditions of position, form, colour, and structure, that it is necessary at once to draw a line between the stamens and all other forms. As a foliar organ of the flower, its definition is not determined, since the sphere is infinitely great here. According to the principle which I have placed at the very beginning of the whole study, namely, the morphological mode of treatment, there are only two possible ways of defining accurately, viz. according to the external and internal forms, or according to the condition of structure. According to the outward form, the externally visible anther-cell, and according to the structure, the development of the pollen, are undoubtedly the characteristics which define the stamen as such: both are so intimately connected that it is unimportant which character is taken. If this character be passed over, scarcely any stamen can be distinguished from the accessory foliar organs of the flower; many — for example, the outer stamens of *Nymphæa*, the stamens of *Canna* — not in any way from petals, &c. And, therefore, the definition must be thus taken: a stamen is a foliar organ of the flower which develops anther-cells, and contains within these pollen. By such a definition we acquire a safe basis for the comprehension of the flower, and the accurate description of the forms. Nothing which does not correspond to this definition (and no other is possible) is a stamen. On such grounds, therefore, it is altogether incorrect and superfluous to speak of castrated or abortive stamens, i. e. of stamens which are not stamens at all. An imperfect perception of the nature of the flower as a whole, lies at the bottom of such expressions. This consists of foliar organs (and axial organs) variously modified, some of which must be stamens (or seed-buds), or the definition of a flower cannot be retained. But the essential nature of the flower does not by any means determine how many foliar organs shall be developed into stamens. Even in particular groups of plants no law can be deduced, seeing that nature forms sometimes one way and sometimes another; but what lies at the basis of the groups, as types, are definite conditions of development, through which are conditioned the number and arrangement of the foliar organs, but not particular modifications of them. These latter are, perhaps, of quite subordinate importance, and may alter in genera and species, nay, even in mere varieties, sportive forms, and monstrosities. What I have particularly to do here, is to reject the anthropomorphic preconceptions of certain ideal types, which float between us and nature, and sometimes perfectly, sometimes imperfectly, attain to a likeness of her; which, however, we entirely carry over into nature, instead of obtaining from her, and which at best can serve but as a make-shift,

until the correct expression of the real common character of a group of forms is discovered. This expression can, and will, only be given by the history of development; and if we wish to understand ourselves and nature, we must now unconditionally give up that clumsy method of preconception. And thus we must establish and maintain in the special case, that nothing which has not an anther-cell and pollen is a stamen, but another form of the foliar organs of the flower, which we are by no means entitled to refer to that particular form. If we take the *Commelinaceæ* as an example, it is part of their general character to develop five tri-merous circles of foliar organs in the flower; the particular group is characterised by the development of the two outer into calyx and corolla, of the innermost into a germen; but it lies in the character of the family that the two intermediate are sometimes all, sometimes partly, developed into stamens, and that in the latter case the remaining foliar organs assume peculiar forms, which however are not stamens. Now, these six organs are all called stamens, and it is added that the anthers (consequently the sole exclusive character of the stamens) are wanting; in this the character of the family is maintained for all: but does the similarity in different plants lie in our imperfect mode of description, or is it not rather in the plant itself? If the latter were not the case, all our systems would be but a childish game with our words. Such a mode of describing a family is therefore entirely superfluous, so soon as the character of the family has been correctly unfolded. In this example the reference is to the analogous position in different genera, and the position in one and the same circle, from which it is presupposed that all its foliar organs must be developed in a similar manner. But the last is just as much as the first, an empty prejudice; here there is, indeed, some loop-hole to creep out at, since the accessory stamens which are formed are by no means so strictly characterised organs as to make the term *stamina castrata* at once evidently inapplicable; but in *Canna exigua* (see Plate III., figs. 12—20.) we have the most striking instance of the entire perversity of this mode of conception, where, in the inner circle of leaves, one is abortive, one becomes the stamen, and one the style. If this circle of leaves were described either as a staminal circle or a carpellary circle, a monstrous Phanerogamous plant would be produced, in which was *typically* suppressed an organ without possessing which it cannot be a Phanerogamic plant at all.

I next turn to the analogy of the stamen with the sporophyll of the higher *Cryptogamia*. An unprejudiced examination renders it manifest that the latter is a true foliar organ, in which determinate cells become parent-cells, which, after the formation of four spores, are dissolved, so that the spores, in their peculiar form of simple cells, invested by a peculiar secreted layer, lie free in certain cavities of the leaf previously filled by the parent-cells, and, by the regular rending of the walls of these cavities through desiccation, become scattered. We find this structure perfectly identical in the phanerogamous anther. I have, in earlier pages, as well as in the paragraphs, remarked upon the analogies, which may be carried out even into individual cases, between the sporophyll and the stamens, more particularly in the *Cycadaceæ* and *Coniferæ*. We are unfortunately destitute of any account of the development of the stamens of the *Cycadaceæ;* but, familiar with the development of other forms, we may tolerably safely come to a conclusion in this case. In *Cycas*, on a woody axis with abbreviated internodes, we find a number of foliar organs,

on the back of which arise a number of little cellular masses, and these become (sessile) capsules in which the pollen grains are developed. That the foliar organ is here developed into a woody scale is an inessential matter of subordinate importance. A similar structure would not be impossible in a Fern, but would merely give a generic distinction. Thus, in *Cycas* we have all the essential characters of the sporophyll of the Fern; and *Cycas* would be a Fern, if a strict boundary were not drawn by the peculiarity of the development of the spore (or pollen grain) into a plant. In the same way, and in a still higher degree, holds the analogy between the stamen of *Taxus* and the sporophyll of *Equisetum*. Disregarding the remnants of the parent-cell, which in the latter adhere to the spore, not even a generic distinction could be drawn between the two structures, if the development of the pollen grain in the seed-bud in *Taxus* did not again enter into the question. The capsule at the base of the leaf of *Lycopodium* also corresponds naturally to the three anther-cells of the base of the leaf in *Cunninghamia sinensis*, Rich. That the latter are formed on the under, the former on the upper, surface of the leaf, can make no essential distinction with the frequent exchange from *anthera antica* to *a. postica* in the same family. If we then trace the stamens from *Cycas* through *Zamia*, *Araucaria*, *Agathis*, *Cunninghamia*, and those of *Taxus* through *Juniperus*, *Thuja*, and *Phyllocladus* to *Pinus*, we find in both series a gradual transition to a simple form, which then becomes the fundamental type for all the rest of the *Phanerogamia*, and may at once, by comparison, but more safely still by following out the development, be traced back in a definite manner to the modified stem-leaf. This phanerogamic type consists merely of this: that the two lateral halves of a leaf, at the sides of the mid-rib (the connective), develope into chambers, in which two groups of parent-cells, separated by a layer of cellular tissue, form pollen, so that every anther is typically an *anthera bilocularis, quadrilocellata*. I shall have to speak more at length regarding the apparent deviations from this structure in the following paragraphs; in this we have merely to do with the definition of the idea and the external form.

The last point requiring notice relates to the differences of the external form of the stamen. I have here, as in all other cases, confined myself to the indication of the outline of the directions which these subordinate variations of form may take. Here, again, the different denominations of the forms are not signs of different ideas, but serve for empirical description, and therefore are to be understood as pictorial expressions, according to the meaning of the words; they are therefore by no means fixed things in the science, but undergo constant extension and correction, as the art of observation and empirically describing, in science in general, becomes developed, or as an individual gifted with a special talent for this advances it. No Botanist is tied down to such terms as *cucullus*, *calcar*, *appendix*, &c., when once he hits upon an expression which describes these forms more aptly, and in accordance with the impression they make; and no confusion in science can arise *from this*. It does, indeed, bring confusion into science, and makes a scientific unity in nature altogether impossible, when a Botanist applies the same terms to fundamental and derivative forms; for instance, to actually independent foliar organs and to their appendages, since here the question is no longer a more or less perfect success in conveying the impression, but a confusion of the definitions deduced from the essential nature of the object.

For my purpose it is merely important to indicate how the different derivative modes of appearance are connected with the fundamental organ, the leaf, and its forms, and originate therefrom, not merely according to the idea, since that is of no use to the unity in nature, but in real metamorphosis, through gradually increased development of this or that region, or this or that portion of the cellular tissue. We must especially look to the most multiform development of the connective, from which arise forms that, when perfect, appear altogether incapable of being referred to the fundamental form of the modified leaf, and yet, when the development is traced, are easily deduced from it. *Celsia cretica* may serve as an example, in which the stamen is perfectly regular in the very young bud, and consists of a filament which passes above into a narrow connective, bearing two longish anther-cells on its two borders; the connective gradually expands in its lower part, and particularly on one side; thus the base of one anther-cell becomes gradually removed from the base of the other, and so far that, since the summits of the chambers always remain in contact (they merge into one here, of which hereafter), in the fully developed stamen the two anther-cells lie in a straight line, and it appears as though only one cell existed on one side of the connective. In a similar manner the strangest forms, as in the *Cucurbitaceæ* and *Philydraceæ*, are readily referred to the fundamental form, when we trace back their gradual development.

It is most remarkable that, with all the other great similarity of the conditions of form of the normal leaf, no true articulation in the continuity of the staminal leaf occurs. *Berberis*, usually named as an example of this, I have neglected to examine. In the *Compositæ* there exists merely a very gradually appearing difference in the cellular tissue at determinate points, which, far from corresponding to an articulation, depends, on the contrary, on a somewhat increased thickening of the cell-walls. In *Mahernia* and *Vinca* there is no trace of an articulation. Never, so far as I have yet been able to examine, does there exist an articulation between anther and filament. The latter is, indeed, when it passes into the anther, often very thin, readily bent, and readily torn away; but there is never a layer of cellular tissue formed differently, breaking the continuity of the structure; the anther and filament never separate spontaneously here.

On the other hand, the stipulary structures are very perfectly developed, and exhibit forms which are often enough mistaken. They appear most remarkably in the *Amarantaceæ*. Nothing is more easy than to trace out the origin of the pretended corona from the blending of the stipules of the stamens in this family, and the perfect forms exhibit every possible transitional condition. The unscientific inconsequence of descriptive terminology is here again most strikingly manifest. So long as the stipules are only partly blended, the terms are: *filamento trifido lobo medio antherifero;* if they are wholly coherent, the two blended lobes are called *stamina sterilia;* if they are diverted to the inner side, so as to escape a superficial examination, as in *Celosia*, it is even written *staminodia nulla.*

§ 155. The condition of structure plays a very important part in the nature of the stamens. The filament, when present, and its appendages, have almost always the structure of petals, consisting of very delicate cellular tissue, filled sometimes with coloured, but more frequently with colourless sap, and having large intercellular

spaces, filled with air, which gives them a snow-white appearance. The appendages of the filament and the connective exhibit like characters. A simple vascular bundle usually runs through the filament and the connective; but not unfrequently the vessels are wanting, as in the case of the *Amarantaceæ*. The vascular bundles are never ramified, excepting in the case of the lobed or pinnate stamens, and then a bundle enters each lobe. The epidermis is here, as in the petals, an intermediate structure between epidermis and epithelium; it presents sometimes, though seldom, stomates, and frequently regular, elegant, and partially brightly coloured hairs.

In the *Apocynaceæ* a little group of hairs is exhibited beneath the anther, upon the upper surface of the filament, in which a quantity of viscid matter is secreted, so that by these adhesive tufts of hair the stamens adhere firmly to the large stigmatic body, and thus render spontaneous fertilisation impossible, since the surface destined to receive the pollen is below the point where the stamens and stigmatic body are connected. The anthers also sometimes secrete a viscid substance, by means of which they adhere amongst themselves, as in the *Compositæ* (here it is perhaps formed by the solution of the secreted layer of epidermis), or they cleave to the body of the stigma, as happens in some of the *Apocynaceæ*.

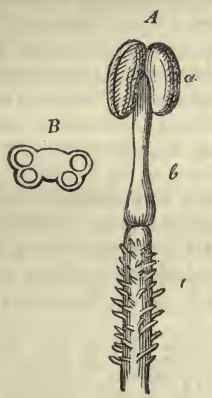
The development of the epidermis into surfaces secreting nectar is also frequent here, especially on the appendages at the bottom of concave forms, at the points of the stipules of the *Lauraceæ*, &c.

Far more important is the structure of the anther. Originally this is formed of quite uniform, delicate-walled cellular tissue; soon, however, after the loculi become externally characterised as incipient expansions, two layers may be distinguished in the cellular tissue, namely, that which is destined to form the walls of the thecæ, and that which is appropriated to the formation of the parent-cells of the pollen. Between these exists another thin layer of cells, which at the time of the perfect formation of the pollen becomes dissolved and absorbed, so as to ensure for the pollen the free space requisite. In all three layers a constant development of cells within cells goes on until the completion of the entire organ, whereby the volume is increased, and the form of the anther, which was developed in its regular manner as a leaf from the axis, is perfected, but not changed. The outer layer of cellular tissue originally clothed with a layer of epithelium, developes this into a structure intermediate between epithelium and epidermis, not unfrequently provided with stomates. The connective sometimes exhibits hairs, the thecæ seldom. Sometimes the epidermal layer is thickened at its outer edge by the presence of a layer of cells elongated perpendicularly to the surface, so that it forms a projecting border (as in *Gladiolus*, *Cassia*, *Passiflora*, &c.) Perhaps, with the sole (?) exception of plants flowering under water, one or more layers of spiral fibrous cells exist in all anthers, but in various modes of arrangement. Usually only one or two layers of

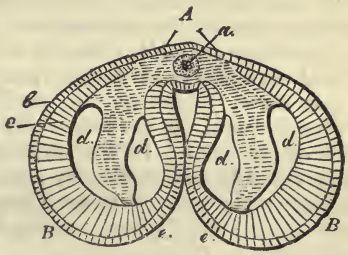
cells, which form the substance of the walls of the thecæ, beneath the epidermis, are developed in this way; more rarely, merely the epidermis; or, again, the entire parenchyma of the anthers, with the exception of the epidermis and the vascular bundles, is the connective.

To illustrate what has been stated in the foregoing paragraphs, I will here introduce figures of the stamen of *Euphorbia* (fig. 205. *A*), with the cross section of the anther (fig. 205. *B*), and a cross section of the anther of *Neottia picta* (fig. 206.).

205

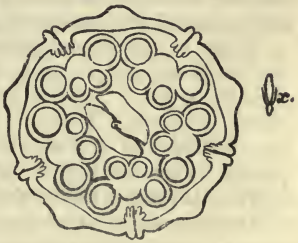



206




The connection of the anthers in the *Compositæ* is usually very incorrectly termed blending. In its early state, each anther possesses its own perfect epidermis; and at a later period the cells of the different anthers are only found adhering to one another on account of secreted matter (fig. 207.), and not truly confluent with one another.

207




I have nothing further to add upon the structure of the filament; this part of the stamen is indeed the least important: but I have other observations to offer on the structure of the anther; and I beg further to refer the reader, for elucidation, to Plate IV., with its explanation.

In that form of the anther which occurs

[205] *Euphorbia Lathyris.* *A*, Male flower: *a*, anther, consisting of two halves (*thecæ*), which retreat from each other in the lower part, and leave the connective free; *b*, filament; *c*, pedicel. *B*, Cross-section through the anther: on each side of the thick connective are two loculi, separated by a septum.

[206] *Neottia picta.* Cross-section through an unopened anther. *A*, Connective. *B*, The halves of the anther, or *thecæ*: *a*, vascular bundle of the connective; *b*, epidermis; *c*, walls of the four loculi (*d*), formed of spiral fibrous cells: the loculi are arranged in pairs, which are divided by the cellular tissue of the partition-wall (*septum*); *e*, the place where the septum separates from the walls, and where this splits, thus throwing the loculi open.

[207] *Actinomeris alternifolia.* Cross-section through a flower-bud (*x*, of natural size).

most frequently, two simple perpendicular rows of cells are very early distinguishable in each theca, from which the pollen is developed. The remaining cellular tissue of the anther may be divided into three groups: 1. That forming the connective and the septa between the fore and hinder loculi; 2. That forming the outer walls of the cellular tissue forming the thecæ; and 3., That lining the thecæ, subsequently absorbed, and mostly elongated in a radial direction. Of these different cellular tissues, only the two last portions (2. and 3.) progress in development by independent cell formation, after the staminal leaf is put forth from the axis. The cellular tissue of the connective once existing in its rudiments does not multiply its cells, but only expands those which are already present, and changes them in manifold ways. The distribution of the cells originally formed in the anther among these three groups exhibits great varieties. Sometimes the largest portion of the original or fundamental cells (as occurs in *Berberis vulgaris*), and sometimes the smallest portion of them (as in *Tropæolum minus*), are employed in the formation of the connective. In consequence of such arrangement, the thecæ exhibit varieties of form, either appearing as four cylindrical cavities (as in *Tropæolum minus* and *Sparganium simplex*), or as four scarcely concave, very shallow cavities (as in *Berberis*); or, as is very frequent, as cavities somewhat deeper, but strongly inclined together at the sides. In the last case, the septum often enters, as a ridge, very deeply into the cavity; as is seen in *Canna* and many other of the *Scitamineæ;* for instance, *Costus* and *Calathea*, in almost all the *Solanaceæ*, &c.; and, in less striking degree, in *Cerbera Thevetia;* and, inconsiderably, in *Gentiana lutea.*

The common supposition, that these projecting ridges are the rudiments of new septa, involves the false presupposition that the septa in general grow from the connective out into the loculi; but, in fact, they exist earlier than the loculi, and are merely the remnants of the parenchyma which has not been converted into pollen. The common statement, that the thecæ have grown to the connective, arises from an equally false perception of the natural condition. In the transitory cellular tissue of the third group, the newly arising cells are both radially and tangentially arranged; in the cellular tissue of the walls, on the contrary, of the second group, they are only tangental; by which means the walls expand towards the surface, and the thecæ enlarge, and continually acquire greater capacity, as the gradual development of the pollen demands. Hence it happens, also, that the little furrow which in the rudiment of the anther is actually the edge of the leaf, at a later period forms the bottom of a deeper furrow, since, as the edge of the septum, it cannot follow that expansion.

Towards the time of the completion of the development of the anther, a part of the cellular tissue of those plants flowering above water is converted into spiral-fibrous or porous cells (see fig. 206. *d*); which cells, or how many, are thus converted, is matter of the greatest variety. Sometimes the change only occurs in the epidermis alone remaining of the outer walls, as in *Lupinus;* more commonly, however, this remains unchanged, and one (e. g. *Compositæ*) or more (many *Liliaceæ*) layers of the outer walls beneath the epidermis become spiral-fibrous cells, usually

The five lobes of the apex of the corolla are applied together by their edges, surrounding five stamens which alternate with them, the transversely-cut anthers of which are only in contact by the posterior loculus of each side, which adhere together. Within are exhibited the two arms of the style in cross-section.

extending to the entire expansion of the outer wall of the anther, sometimes scarcely to half of it, on each side of the longitudinal furrow. Sometimes this spiral-fibrous layer extends under the epidermis, over the anterior surface of the connective (as in *Pachysandra procumbens*), or over the posterior surface (as in *Hyoscyamus orientalis*), or over both (as in *Gentiana lutea* and *Erythræa*). Sometimes such a layer lines each loculus on all sides (as in *Strelitzia farinosa* and *Hippuris vulgaris*), either leaving the septum free or actually forming it; sometimes a layer extends round each pair of loculi lying on one side, with an unaltered septum (as in *Calathea flavescens*), or making a curve in it, without entirely metamorphosing it (as in *Costus speciosus*). Finally, in very rare cases, all the cellular tissue, even up to the vascular bundle of the connective, is converted into spiral-fibrous tissue. This multiformity, left unnoticed by Purkinje*, shows the manifest inapplicability of the terms proposed by him—*exothecium* for the epidermis, *endothecium* for the spiral-fibrous layer. The walls of the small loculi of *Cycas revoluta* are formed entirely of a thick porous cellular tissue. In the *Compositæ* the connective is formed of elegant porous cells, as are the generality of the crest-like appendages of the anthers (e. g. in the *Centaureæ*).

The formation of the pollen takes place in the following manner: in the interior of each rudimentary loculus a process of development commences within a soft row of cells, through which, in the common form of the anther, a cylindrical string of cells, more or less in number, the parent-cells, are gradually formed. In each parent-cell the granular mucilaginous contents divide, simultaneously with the appearance of a cytoblast, into four portions, which quickly become clothed by four cellular membranes; or it may be that originally two such cells are formed, and within these again other two in each. These cells enclosed within the parent-cells are special parent-cells. Then, by means of the secretion of a gelatinous layer over the internal surface, these parent-cells and special parent-cells become very much thickened, and a simple cell (the pollen-cell) is produced simultaneously in each special parent-cell. This, in all plants except those flowering under water, secretes upon its outer surface one or more layers, forming the external pollen membrane, which assume, in some cases, peculiar and remarkable forms. During this last perfecting of the pollen, the parent-cells and the special parent-cells are dissolved and absorbed. In many Monocotyledons, especially *Liliaceæ*, the product of the solution of the parent-cells is a clear or dark yellow fluid, of glutinous or oleaginous (?) nature, which adheres to the external pollen membrane. In the *Onagraceæ*, in the parent-cells or special parent-cells (as in the *Equisetaceæ*), a spiral thickening layer is formed, which is not dissolved with them, but adheres in long threads to the perfect pollen granules. A part of the product of the solution of these cells is frequently viscid, and glues the four pollen granules belonging to one parent-cell firmly together (*pollen quaternarium*); sometimes it unites only two (in *Podostemon*), and sometimes a greater number of granules, (in some *Acacias*, for instance,

* De Cellulis Antherarum Fibrosis. Breslau.

*A. lophantha*). In the *Orchidaceæ*, the entire product of the solution of the parent-cells and special parent-cells is viscid, and glues all the pollen granules in a mass, and is easily recognised between them, as a tough substance, capable of being drawn out in threads. In the *Asclepiadaceæ* it appears that only the parent-cells are absorbed, and that at a very early period; the special parent-cells are not absorbed at all, but adhere closely to one another, and so form, out of the whole mass of pollen a loculus, or small cellular body, which appears clothed with a special membrane, since in the outermost layer of the special parent-cells no pollen granules are developed. Probably there exists in all the cells, from the parent-cells to the pollen granules, a circulation of sap (in the latter most certainly, in the young condition), the currents of which form reticulations on the cell-wall.

I have, in the preceding account, given the history of the development of the pollen, essentially in accordance with the excellent investigations of Nägeli*, as I have nothing more complete of my own to oppose to it. Let Plate IV. and the explanation be compared with the preceding. I by no means suppose that what has been said will be found the complete settlement of the entire matter, and I cannot withold some thoughts which strike me with regard to the formation of the cells. There are two difficulties which certainly nowhere oppose so great a barrier to the completion of investigation as here; namely, the attainment of perfect stages of development, and the correct arrangement of them in their proper series. I will offer the following objections to Nägeli. I will first mention that I have convinced myself, both in the parent-cells and the special parent-cells (in the cases of *Pepo*, *Passiflora princeps*, and *Arum maculatum*), and also in the young pollen-cell (in the cases of *Lupinus*, *Larix*, *Pinus alba*, *Juniperus*, *Richardia æthiopica*, *Arum maculatum*, and *Fritillaria imperialis*), that the cytoblast is clearly to be recognised as parietal (sometimes even in the pollen-cell which has sent a tube into the nuclear papilla of the seed-bud). In *Fritillaria*, two kinds of cytoblasts are easily to be distinguished, those which give the origin to the pollen-cells, and lie embedded in the walls, and those which form later in the pollen-cells and here, as is not rare in the pollen-grain generally, give origin to a transitory process of cell-formation.† A second point, wich appears to me important, is that I have frequently observed, between the period of the existence of the empty parent-cells and their regular division into two or four special parent-cells, free cytoblasts floating among the granular contents of the parent-cells (*Passiflora princeps*), and I have seen also this accompanied by very delicate young cells with cytoblasts on the walls (in *Passiflora princeps*, *Pepo*, and *Rhipsalis salicornioides*). In the last-named plant I observed all the transitional stages between free cytoblasts and the perfect formation of the special parent-cells (or the pollen-cells ?); in other plants I have not yet succeeded in such complete observation. Finally, I must observe that the entire assumption of special parent-cells appears to me questionable. It is no matter of doubt that in the stage near maturation, each pollen-cell appears surrounded by a tolerably thick gela-

* Contributions to the History of Development of the Pollen of the Phanerogamia (Zur Entwick. des Pollens, &c.). Zurich, 1842.

† Nägeli, loc. cit. pp. 20, 21.; Meyen, Physiologie, vol. iii. p. 186.

tinous membrane; and that each four lie thus in a thicker gelatinous parent-cell, which is manifestly such from its origin. But the so-called special parent-cells are not easily distinguished either from the parent-cell, or from one another, or from the enclosed pollen granules at this period. Their origin may, indeed, be other than that assigned by Nägeli. The following appears to be equally probable. In the parent-cell are formed, according to the laws of development, four pollen-cells; whilst these expand, the granular contents of the parent cell are gradually dissolved into gelatine, in which the pollen-cells then lie imbedded. By this pressure of the expanding pollen-cells, a portion of the gelatinous substance is thickened or condensed into a membrane around and enclosing each, and thus forms the so-named special parent-cells.

Where, on the contrary, the parent-cells first divide into two cells, two special parent-cells are really formed, but in the same manner as I have just described of the pollen-cells; and in each of these special parent-cells two pollen-cells are formed in the same way. It would be in harmony with this that a distinct *pollen binarium* occurs, as in the *Podostemaceæ*, which indicates the closer relation of the pollen-cells. Only continued and careful investigation can decide whether Nägeli's excellent observations, as he has related them, are to be regarded as complete, or, according to the hypothesis I have given, to be brought into agreement with other processes of cell-formation.

On the other matters mentioned in the paragraphs, I have only to add that I have found Nägeli's observations respecting the order in which the parent-cells and the special parent-cells are dissolved, and upon the external pollen membrane, a secreted product of the pollen-cells, perfectly correct.

The perfect pollen granule consists, as has been said, of the essential pollen-cell, which in plants flowering above the water is clothed with a peculiar secreted layer. This always forms an uniform membrane lying immediately upon the pollen-cell, not unfrequently in a double layer, on which usually appear all kinds of strange projections (the first product of the secretion). Most frequently these little ridge-like projections are connected together in a reticulated form, and often give the external membrane the deceptive appearance of being composed of cells, which the history of development proves not to be the fact. The spaces between the meshes of this net are frequently partly filled with transparent jelly (in *Iris* and *Passiflora*). Sometimes these articularly-connected ridges present very regular, definite areas, giving, in the excessively varied form and arrangement of the pollen grains, the most elegant and beautiful appearance: this is especially the case in the *Passifloræ*. Sometimes, again, the projections appear as minute points, cones, papillæ, curves, or like little towers, either scattered upon the surface or very regularly arranged there (e. g., most elegantly in many of the *Compositæ*, *Scorzonera*, *Tragopogon*, &c.). The substance of this secreted layer is usually yellowish, more rarely tinted with green, blue, or red, and by concentrated sulphuric acid it is only very slowly destroyed (requiring one or two days), and during this the acid often gives it a Burgundy-red colour.

In all pollen granules the external pollen membrane exhibits

certain places, either like slits or in well-marked circles, where it is either entirely wanting, or becomes so exceedingly thin as to escape the eye. The number and arrangement of these places is very different; thus the generality of Monocotyledonous pollen granules have only a longitudinal slit (as in *Lilium*); some Dicotyledons have very many (as *Polygala*); the generality of Dicotyledonous pollen granules have three circles uniformly distributed at their equators (as in *Centaureæ*), or four placed towards the angles of the tetrahedron, or they have a large number (as *Polemonium cœruleum* and *Ipomœa purpurea*). These openings are not always free, but sometimes covered by a lid-like portion of the secreted layer, which is entirely separated from the rest of the membrane (as in *Pepo*).

The contents of the pollen-cells are originally almost purely granular, with a small quantity of fluid; by degrees, however, the granules are dissolved, and the thin contents become watery and almost transparent, whilst the granules, still remaining undissolved, appear as globules of mucilage. Towards the time of the maturation of the pollen granules, these increase in size, and other small granules appear amongst them of some undetermined substance, coloured yellow by iodine (*Inuline ?*), and minute globules of oil; very frequently, also, starch granules, in greater or smaller number, sometimes of peculiar form (e. g., in the *Onagraceæ*), and always differing much in size in the same pollen granule. By their presence the fluid becomes more concentrated, losing water and acquiring an extraordinary endosmotic power, even towards acids, on the application of which it expands, the pollen-cell bursts, and its contents, being protruded, coagulate into the form of an intestine. The pollen granule, which towards the close of its development is very much expanded, contracts again a little when quite mature, on account of the loss of the water, and forms considerable folds in the direction of the slits or pores, which are again effaced by the absorption of water. The movement of the contents in reticularly-connected currents has ceased in all the mature pollen granules (with the single exception, as yet known, of the long cylindrical pollen granule of *Zostera marina*); but instead of this, the various granular contents of the pollen-cell exhibit active molecular motion: this is often seen while the contents are still within the pollen-cell, and always after they are expelled, even in the pollen of old specimens in herbaria, and after the operation of tincture of iodine.

We have received from Fritsche, in his work on the Pollen, published in St. Petersburgh in 1837, a collection of most careful and accurate investigations respecting the condition of the external pollen membrane in its perfect state, to which I must here refer. In some plants he distinguished three several layers in the outer membrane of the pollen granule. I do not think myself obliged to accept his terminology, since it is not in accordance with the most recent investigations. Here the pollen-cell and the secreted layer are opposed to each other; this last may be single, or it may be divided into three layers, but it is always opposed to the pollen-cell merely as a single whole. The individual layers, however,

when they are present, are best defined as first, second, and third layers. That the external pollen membrane never consists of cells, will be self-evident after the manner of its origin is known; but Meyen had already corrected this error, which arises from the very deceptive appearances.

The doctrine of vegetable spermatozoa is now, I hope, gradually dying away. A man must be blinded indeed by old prejudices if he will continue, after the very complete investigations of Mohl, to hold the remote analogies between the antheridia and the anther. I have already shown that in *Phanerogamia* the representatives of these are to be sought in a very different place. The granules (generally starch) taken for spermatozoa have, indeed, lost their life in Fritsche's tincture of iodine, since their evidently purely physical molecular movement remained undestroyed.

It appears to me altogether superfluous to enter further upon this point; Meyen * gives the whole literature, which has now merely a historical value. Fritsche † has completely settled the matter, and every unprejudiced observer may convince himself with ease of the completely untenable nature of the wonders formerly spun out, especially by Meyen. The confirmatory observations of Nägeli on this point are also of great value. ‡

At a determined time the thecæ of all anthers open in one fashion or other, in order to permit the dispersion of the pollen, just like the sporocarps of *Cryptogamia*. The manner in which this takes place varies very much. The thecæ of the anthers of the *Cycadaceæ*, which are small in size, two or four in number, and united into a little oval, capsular form, are rent open by a longitudinal slit; the thecæ of *Juniperus*, *Taxus*, and their allies, open exactly like the sporocarps of *Equisetum*. I am unacquainted with the manner in which the anthers of most of the exotic *Coniferæ* burst. In our native *Abies* (*Pinus* and *Larix ?*), and in all the *Asclepiadaceæ*, only one loculus is formed at each side of the connective, both open, whilst the wall is torn away in the middle line from the connective, therefore with two longitudinal slits, one for each loculus. The outer wall of the loculus, which thus becomes disengaged, and which is dry and elastic, is termed the valve (*valvula*); and because only two valvulæ are to be distinguished, only one long cleft is spoken of, *anthera rima longitudinali unica dehiscens*.

In many *Caladieæ*, in *Ceratophyllum*, and other plants, at the time of the ripening of the pollen, a canal is formed (by destruction of the cellular tissue ?) to the summit of the anther, through which

* Physiologie, vol. iii. pp. 178—196.

† Loc. cit. suprà.

‡ Gottsche (on Haplomitrium Hookeri, Act. A. L. C. N. C. xx. i. p. 304.) has a strange polemic against me, referring what I say regarding the contents of the pollen of *Phanerogamia* to the contents of the antheridia of the *Cryptogamia*, because he cannot overcome the prejudice that the anthers of the *Phanerogamia* and the antheridia of the *Cryptogamia* are the same organs. He is guided here solely by the word anther; and this very mistaken argument may show to him, as an example, how wrong he is in saying, at p. 297., that by the term antheridium he knows neither more nor less than by the term anther. Of course, one understands more by it: the different word tells us that we have to do with a different thing, and must not mingle matters which are not the same. The whole argument is the more strange, since I myself had published, at least long before Gottsche, some contributions to the knowledge of the spiral filaments in the antheridia of the Mosses and Liverworts, and their motion.

the pollen is emitted (*anthera poro dehiscens*). In almost all the rest of the Monocotyledons and Dicotyledons, the basis of the structure is the origination of two loculi on either side of the connective; this then forms the septum between the two halves of the anther, a layer of cellular tissue running from this towards the two sides divides each half into a fore and hinder loculus. Rarely (as in *Viscum*) cross partitions form additional horizontal septa. In the *Piperaceæ*, *Malvaceæ*, *Solanaceæ*, *Cucurbitaceæ*, and perhaps some other families, the two fore and hinder loculi become blended into one at the summit of the anther; if, then, through great expansion of the connective, the bases of the two halves of the anther are gradually brought into straight, or almost straight lines (as in *Peperomia*), we have an anther really, though scarcely apparently, formed of two thecæ, from which the case (frequent in the *Scitamineæ*) where only two loculi are formed on one side of the connective (the *anthera dimidiata*), must be carefully distinguished. The part of the wall which extends between the connective and the septum is also always termed the valve. Most of the varieties which are commonly distinguished in the anthers depend, in the first place, upon the spreading out of the thecæ through the expansion of the connective, and the time and manner of the disengagement of the valves. They commonly remain attached to the connective, and whilst yet connected together tear themselves away from the septum, which is thus, either in part or entirely, destroyed (the *anthera bilocularis* of descriptive botany). Sometimes the disruption happens later, and they separate almost simultaneously from each other, as in *Tetratheca* (*anthera quadrilocularis*). The separation of the valves from each other usually begins above. If it be confined to a small portion of their length, as in many Grasses and in the *Ericaceæ*, the anther is termed *anthera poro* (*spurio*) *dehiscens*; if the separation extends to the whole length, the anther is said to be *utrinque rima longitudinali dehiscens*. Very rarly the valves separate, connected together all round, or upon the anterior side of the connective (the *anthera unilocularis* of descriptive botany): this characterises the family of the *Epacridaceæ*. A very aberrant structure occurs in two families very far removed from each other, namely, the *Berberaceæ* and the *Lauraceæ*. In these two the valves become free in the entire circumference, with the exception of one small point at the summit of the loculus, and curl back from below upwards (*anthera valvulis dehiscens*). In the *Lauraceæ* the additional peculiarity occurs, that of the four original rudimentary loculi, the two hinder ones either shrivel away, or the loculi become so displaced by the unequal expansion of the connective, that at last, instead of lying one in front of the other, one is placed on the top of the other.

It is a proof of the dreamy spirit which prevails in our science, that, even with respect to superficial knowledge of the structure of this most important of the organs, the anther, the truth has not yet been arrived at. It is, in fact, no better than if zoologists should be yet engaged in

contending, whether the human heart contains four chambers or only one,— and how little skill is required to make a transverse section of an anther in a rather young bud! In the *Compositæ* (fig. 206.), there are four-celled anthers in which the valves of the hinder loculi are glued together, and commonly burst open at each side by a longitudinal slit.

Almost every patch of turf affords material for the investigation of this condition in *Bellis perennis:* in the Zinnias, Sun-flowers, &c., merely a tolerable lens is required to make the matter out readily, and yet in so simple a thing as this Link says*: "Originally the anthers are closed, and exhibit a five- (instead of *twenty-*) chambered tube, then the inner borders (which are these?) separate, and the tube becomes one-chambered." I think it would be impossible to find a notion more contradictory of nature, and to represent it more confusedly.

The anthers of most plants, as has been said, have originally four loculi, not, as is usually said, on account of the incurvation of the borders of the valves, but because they secrete four cords of cellular tissue for the formation of the pollen. From this rule the *Œnothereæ*, in particular, do not deviate, though Link ascribes to them anthers with only two loculi from the very first. So also the anthers of *Malvaceæ* are not one-celled on each side, but two-celled. Still less are the anthers of the *Balsamineæ* altogether and in every case one-celled, as Link says†, but perfectly four-celled. Of *Canna*, he says, the anthers appear to be contracted from a two-celled anther, as the suture is compound. The fact is, that in *Canna*, *Maranta*, *Calathea*, *Phrynium*, &c., the anther is perfected only on one side of the connective, but here regularly two-celled, with a perfectly simple and usual suture, and a septum which, according to specific variations, projects more or less, as a ridge into the theca; in the *Scitamineæ*, in the strictest sense (R. Brown), on the contrary, two loculi are perfected on each side of the connective, and in these also the septum projects inwards into the thecæ, sometimes more (*Hedychium coccineum*), sometimes less (*Curcuma aromatica*). The remarkable structure of the valves in the *Lauraceæ* (and in the *Berberaceæ* it is similar) may readily be understood from fig. 208.

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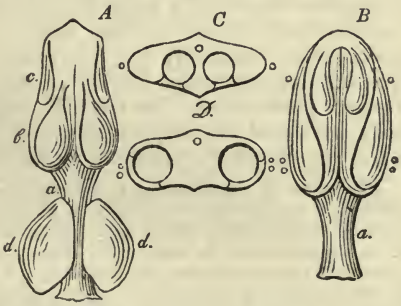


* Elem. Phil. Bot. ed. 2. p. 179. † Loc. cit.

208 *Laurus carolinensis.* *A*, Stamen of the outer circle: *a*, filament; *b*, anterior and lower — *c*, upper and posterior pollen-chambers (*loculi*); *d*, the glands analogous to stipules. *B*, Stamen of the inner circle; *a*, filament; °/₀, lower posterior; °, upper anterior loculi of the loculi. *C*, Cross-section of the anther (*B*) in the level of °°. *D*, Cross-section of the same in the level of °°/°°.

I will now call attention to some peculiarities of the family of the *Orchidaceæ*, which have hitherto remained wholly unexplained. The least remarkable of these is, that the pollen is often formed in more than four (eight to sixteen) different portions, and therefore more than the usual four loculi exist; as in *Calanthe*, *Bletia*, &c.: the most usual arrangement is, however, that in which the anther is regularly four-celled; particularly in all the *Ophrydeæ* (fig. 209.), in which the pollen mass of each cell, from causes unknown to me, becomes divided into many small ridge-shaped pieces (fig. 210.), which are arranged around one large central

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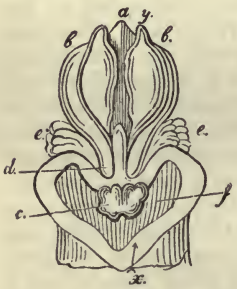


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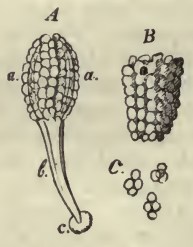


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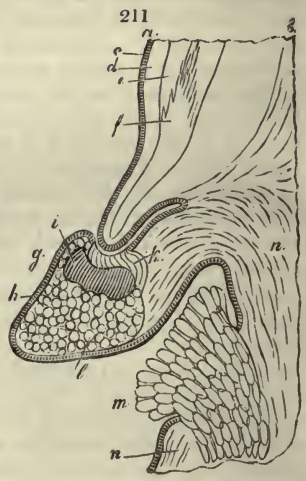


mass of that viscid substance already mentioned above. It not unfrequently happens that the cellular tissue appointed for the formation of the pollen forms a secretion continued as a narrow process into the attenuated base of the anther, sometimes also curving round forward from the broad base, and then ascending into the substance of the valve, as in *Epidendrum cochleatum;* sometimes the connective of the anther is continued forward over the stigma, as a pointed process, the *rostellum;* that cellular tissue sometimes extends up into this. All this cellular tissue, however, subsequently commonly becomes changed into *viscine*, and then it forms the tail-like appendage known as the *caudicula* (figs. 210. *A. b.* 211. *f.*) on the pollen mass. At the lower edge of the anther, commonly glandularly thickened at this point (fig. 209. *c.*), or of the *rostellum* (fig. 211. *g.*), are exhibited frequently at an early period, *beneath*

[209] *Orchis militaris.* The organs of generation of a bud about two-thirds long, after the removal of the perianth. The germen is cut away, as also the lip, so that we can see the edge and the entrance to the cavity of the spur of the lip, the inferior part of which is also removed. *a*, Connective of the anther; *b b*, the two halves of the anther; *c*, the receptacle, still covered by the membrane (the *bursicula*); *d*, the inferior part of the anther-cell, wherein the *caudiculus* is situated; *e e*, the two accessory stamens; *f*, the stigmatic surface. The arrow in the direction from *x* to *y* shows the direction of the section which fig. 211. represents.

[210] *Orchis Morio.* *A*, Pollen mass from one half of the anther: *a a*, the two lobes of the mass, corresponding to the two loculi of one side; *b*, the *caudiculis*; *c*, the *retinacula.* The lobes (*a a*) are divided into many wedge-shaped portions: one of them is much magnified in *B*, and in itself again consists of groups of pollen granules, united in fours.

[211] *Orchis militaris.* Longitudinal section through the central part of the organs of

the epidermis (here termed the peach, *bursicula*) (figs. 209. *c*. 211. *h*.), one or two small groups of cells which become filled with viscine, and are in part dissolved into it (figs. 211. *i*. 210. *c*.). The membrane covering them is gradually decomposed, and they then lie free, and are termed the retinacula (fig. 210. *b*. *c*.); if the epidermal membrane becomes decomposed very early, they are termed *retinacula nuda*. In the last case, the cellular tissue which separates the point of the caudicula from the retinaculum is also decomposed at the same time, and thus caudicula and retinaculum come into union (this also, therefore, happens before the anther opens). In the first case, on the contrary, the two are frequently separated, but so placed, that as the anther opens, the very slightest movement of the pollen mass brings the point of the caudicula into contact with the then always bare retinaculum, so that they adhere together. It is perfectly easy to follow this process in the last-mentioned case, in *Orchis militaris*, and especially easy in the very long *rostellum* of the *Neottieæ*. *Gymnadenia albida* and *conopsea* offer good examples of the other case. The *Orchideæ diandræ* and the *Apostasieæ* exhibit none of these remarkable peculiarities, having their anthers regular, and pollen granules which do not adhere together.

I have never yet succeeded in penetrating the very first stages of the formation of the flower; the little I have seen in *Orchis latifolia* and *Cypripedium Calceolus* gives me ground to presume that only three stamens are ever formed in rudiment, of which, in *Cypripedium*, one is developed in a foliaceous form, whilst in the rest of the *Orchidaceæ*, two are abortive, or appear as two little fleshy scales, which, in consequence of the one-sided, excessive development of the upper floral envelopes (the *labellum*), are pushed to the side of the single developed stamen.

The most incomprehensible structure of the anther, if I have seen it in the true light, occurs in *Caulinia*. Here, both in male and female, a bracteole is developed into a pitcher-shaped organ, which in the female is two-lobed above, resembling a germen with two stigmata; in the male splits up in the upper part on one side, imitating a perianth.

On the little conical body which is embraced by each bracteole, an envelope is formed, in both sexes, in the manner hereafter to be described in the seed-bud; and at this time it is impossible to determine whether *mas* or *femina* is being formed; but then they begin to deviate, and in the *femina* the seed-bud produces a second integument, and becomes inverted, whilst in the *mas* the cone grows up into a large nucleus; and while this becomes invested by the envelope until only gradually a little canal remains at the summit, it is entirely (?) converted into pollen, which then finds an outlet by that opening at the apex. Finally, *Brosimum Alicastrum* also appears to possess a most aberrant formation of anther. The beautiful representations of this in our Botanical works look strikingly like elegant, newly-turned chessmen; and without knowing the structure in nature, one may assert that the pictures have little resemblance thereto.

generation, in the direction of the arrow (*x*, *y*) in fig. 209. *a*, *b*, Lower part of the left half of the anther; *c*, epidermis; *d*, parenchyma of the walls; *e*, pollen mass; *f*, *caudicula*; *g*, point of the *rostellum*, here very short; *h*, epidermis (*bursicula*); *i*, *retinaculum*; *k*, part of the *bursicula*, which is subsequently dissolved, so that the *retiniculum*, now free, comes in contact with the *caudicula*, also set free by the bursting of the anther; *l*, loose, easily separable cellular tissue; *m*, outer surface of the conducting cellular tissue (the stigma); *n*, parenchyma of the disc, forming a style.

### c. *The accessory foliar Organs of the Flower.*

§ 156. Besides those parts of the flower of which we have already spoken, other foliar organs are frequently met with, which, considering their simple structure (scales of varying degrees of thickness) or very aberrant shape, may be regarded as parts of the flower but partially developed. According to their position, I distinguish two forms: 1st, from the outermost floral envelopes to the outermost circle, exclusively, in which stamens are developed, the accessory corolla or *paracorolla,* and its accessory petals or *parapetala;* and, 2dly, from that circle, inclusively, to the germen, the accessory stamens, or *parastemones.*

The accessory corolla consists sometimes of scales, which are either thin and leaflike or thick and fleshy, with their margins sometimes entire, sometimes divided, as in the Grasses, the inner tri-merous circle of foliar organs, of which one member is commonly abortive: in *Vallisneria* the three little scales. More frequently the accessory corolla exhibits very peculiar aberrant forms, which may present the forms of the floral envelopes in miniature, and often distorted, as in the long, thin foliaceous organs in the flower of *Aconitum,* which imitate a long-clawed, spurred perianthial leaf, the horn-shaped accessory petals of *Helleborus, Trollius, Nigella,* &c., the extraordinary little, mostly boat-shaped leaflets of the *Loasaceæ.* I am unacquainted with any instance in which the members of the accessory corolla are coherent. The structure is either very simple, as in the generality of scales, which consist merely of delicate cellular tissue; or it resembles that of the floral envelopes and its appendages. The secretion of nectar at given places is very frequent here, especially in concave forms.

Accessory stamens occur in two ways—either as perfectly free foliar organs, or wholly coherent. *a.* In the first case they are more or less similar in form to the stamens, and often, especially if (as in *Chelone* and *Scrophularia*) they belong to a circle, of which some members are developed to stamens, they are formed exactly like a filament without its anther, as in many *Geraniaceæ:* sometimes they are also scale-like here, as in *Veronica,* where they represent two parts of the four-membered staminal circle.* When they form a proper circle by themselves, they are usually developed as small scales, as in *Pimelea, Gnidia,* &c.

*b.* In the second case, they mostly constitute the so-called inferior ring (*annulus hypogynus*), and are then usually thick, fleshy, and juicy, as in *Daphne, Celosia*†, and *Trapa.* Sometimes this ring is lobed, so as to exhibit the number of its members clearly, as in the generality of the *Ericaceæ:* in *Chrysosplenium* it is eight-lobed; in *Cobæa scandens* and *Convolvulus* five-lobed; or indis-

* This condition also appears to exist in *Lathræa* and *Orobanche.*

† In which this ring has hitherto been wholly overlooked.

tinctly (as in the whole family of *Scrophulariaceæ*). In its fully-formed condition, however, it is more frequently quite uniform, as in *Ruellia formosa*, *Calystegia*, and many *Polemoniaceæ*. It sometimes, also, shares the symmetry of the flower, as in *Gesneria* and *Pedicularis*.

In the matters treated of in the preceding paragraphs, an indescribable confusion prevails, which results from a total neglect of the development. To settle this question at once, is beyond the power of an individual; and it is a subject for research in the highest degree serviceable, and yet by no means of great difficulty, by as comprehensive as possible monographic examination of these structures, and an exhibition of their nature founded on the development, to establish at least a temporary basis, from which then further advance may be made. In the foregoing sections I have only been able to give indications. These structures, as well as the entire series of independent appendages of the floral envelopes and stamens, and a portion of the peculiar forms of the axial organ of the flower, are almost all described under the same names, sometimes as *paracorolla*, with its subdivisions, *corona*, *fornix*, *cuculli*, *cylindrus*, &c., sometimes as *discus* or *nectaria*, sometimes as *staminodia*, &c.; and the question never being mooted, whether parts offering similar appearances may not have very various origin, and what? I have endeavoured to establish the definition of the accessory corolla in contradistinction to the floral envelopes, and thus to render possible a simple and consequent terminology.

For the elucidation of the matter, I give some examples.

In the *Ranunculaceæ* (*Helleboreæ*), I term the external leaves of the floral envelopes the perianth (fig. 212, *A. a. b. c. d. e.*), and the inner ones, which are always diverse in form, and often dwindled in development, the accessory corolla (fig. 212, *B.*). So I term the paleæ of the Grasses the perianth (fig. 213, *A. c. d. B.*), and the scales (*squamulæ*, Rob. Br.) I term the accessory corolla (fig. 213, *C. h. h.*). From these

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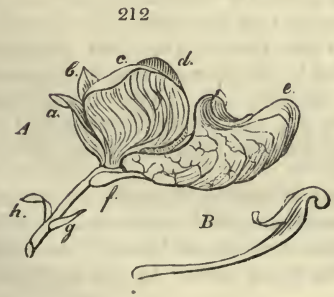


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[212] *Aconitum napellus.* *A*, Flower: *a* to *e*, five perianthial leaves; *e*, hood-shaped; *f*, *g*, *h*, three bracteoles. *B*, Accessory petal.

[213] *Phalaris cœrulescens.* *A*, Spikelet: *a* and *b*, spathe formed of two bractea (*valvæ glumæ*, Auct.); *c*, *d*, one free and two coherent perianthial leaves (*paleæ*, Auct.);

must be carefully distinguished all those dependent organs which have also been termed the accessory corolla, as, for example, the *corona* of the *Narcissus* (fig. 214, *h.*), and the so-called accessory corolla of the

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*Asclepiadaceæ*, which are for the most part only remarkable forms of the filament and the connective of the stamens (see fig. 220.).

All the remaining foliar organs of the flower, from the outermost circle in which the stamens are developed, to the germen, may be embraced under the general term of accessory stamens. A definitive separation of them is impossible, since their forms are continually passing into one another. The scales in the flower of *Pimelea* (fig. 215.) may serve as an example.

Here the history of the development is still too imperfect, especially in the forms which produce the so-called inferior annulus, to allow of our distinguishing those arising from a circle of leaves from those which are a simple extension of the floral axis. In the first case,

*e e e*, three stamens; *f*, a stigma. *B*, The two coherent perianthial leaves, with two nerves (*palea superior*, Auct.). *C*, Pistil, surrounded at the base by the two weakly coherent accessory petals: *h h*, *squamulæ*, Auct.; *g*, germen; *f*, one stigma; the other is cut off.

[214] *Narcissus lætus.* Flower. *a*, Peduncle; *b*, spathe; *c*, bud; *d*, pedicel; *e*, inferior germen; *f*, tube of the perianth; *g*, limb of the perianth, appearing as six free leaves; *h*, corona, formed of six coherent ligules of the perianthial leaves.

the individual rudiments of the leaves are formed quite separately, and always before the carpels: it is by a later process that they become blended together into a ring. In the second case, the ring, or *discus*, originates at once as a perfectly uniform whole, and always after the appearance of the carpels, by a simple extension of the axis already existing, though this may not itself bear foliar organs on this part (as in *Reseda*). This last case exists in the *Boragineæ* and *Labiatæ*, in the discus (the so-called *gynobasis*). *Trapa*, *Convolvulus*, and the family of the *Scrophulariæ*, offer good examples of the first case. But in these another difficulty presents itself, which it will require the most comprehensive examination to conquer; namely, in these there appears to occur either a division into two groups, of which one has four-membered and the other five-membered circles in the flower, or they are both four-membered, and the perfect floral parts of the one group only appear five-membered because the individual members of the same are unequally developed: thus one leaf of the innermost circle will form the unilateral disc, while the other three become stamens, and with one or two leaves of the next circle form the four or five stamens, &c. My investigations of *Pedicularis* and *Orobanche* have led me to this conclusion: the original and always four-divided type is distinctly present in *Veronica*, in which the two leaves of the innermost circle form stamens, and the two others an unilateral disc *: similar conditions also occur in the allied families; and a more close investigation would include the *Acanthaceæ*, the *Pedalineæ*, &c., within the circle of investigation.

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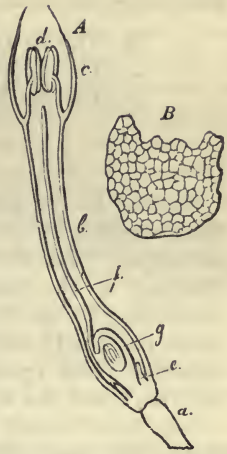


## D. The Rudiments of the Fruit.

§ 157. The seed-bud, which is the only essential part of the rudiment of the fruit, may be either naked, or enclosed in a receptacle, which last is termed the pistil. When it is present it consists of two parts; a cavity which encloses the seed-bud, the germen; and an external opening peculiarly modified, the stigma: sometimes the germen is elongated beneath the stigma into a longer or shorter tube, termed the style. The seed-buds are attached, at determinate places, in the germen, where a part is often so characterised as to be particularly distinguished as a peculiar organ. This part is called the spermophore. For the

* In *Calceolaria* there are only two tetra-merous circles, the outer of which becomes calyx, while in the inner the upper and lower leaf become corolla, and the two side ones stamens.

215 *Pimelea decussata*. *A*, Longitudinal section through the flower: *a*, pedicel; *b*, tube; *c*, limb of the perianth; *d*, two stamens; *e*, accessory stamens; *f*, style; *g*, germen with the seed-bud. *B*, An accessory stamen, much magnified.

better comprehension of the conditions and of their internal connections, I will proceed with the consideration of them in the following order: —

*a.* The Pistil.
*b.* The Spermophore.
*c.* The Seed-bud.

### a. *Of the Pistil.*

§ 158. To the pistil I only refer those parts which contain actual cavities, in which one or more seed-buds are subsequently developed. In this sense of the word, the pistil is absolutely wanting in the *Coniferæ*, the *Cycadaceæ*, and the *Loranthaceæ*. According to the fundamental organs of which the pistil is formed, three principal kinds are to be distinguished. These are the true superior pistil (*pistillum superum*), the inferior germen (*germen inferum*), and the stem-pistil (*p. cauligenum*). The first is formed from one or more foliar organs; the second, in its lower parts, from the pedicels, in its upper part frequently from foliar organs; the third originates entirely from axial organs, above and internal to the floral envelopes. A foliar organ, in so far as it contributes to the formation of the pistil, is termed a carpel (*carpellum*). The following cases merit a more detailed explanation.

I. *Of the superior Pistil.* — The pistil formed from a carpel originates as a leaf, which, in the first instance, expands like a leaf; then its edges gradually grow together from below upwards; the lower (*vaginal*) portion, by growing together, becomes a hollow body, and forms the germen; the upper part, not grown together, but expanded free, forms the stigma; the intermediate portion (the petiole), when present, growing together into a tube, communicating with the germen and opening externally at the beginning of the stigma, forms the style (as in the *Zea Mays*). When formed in this manner, the whole is a simple, one-membered pistil (*p. simplex monomerum*). In this case, the germen is one-celled only (*germen uniloculare*). In some cases, by a cellular growth from the inner surface of the surrounding walls of the germen, false septa are formed; these are spurious dissepiments (*dissepimenta spuria*), by which the germen is divided into spurious compartments (*germen spurie pluriloculare*), as in the *Araceæ*.

If the pistil is composed from several carpels, these may form

*a.* Either into pistils, in the manner just described, and remain separate = the multiple, monomerous pistil (*p. plura, monomera*), or, standing in one or more circles *, become coherent with one

* Lindley's explanation of the structure of the fruit of *Diplophractum* (Elements of Botany, 1841, p. 503.) appears to me very adventurous; at any rate we have as yet no accurate knowledge of the germen at the period of flowering, and therefore the whole is at present altogether hypothetical. It seems much more probable to me that the five inner chambers are by no means fruit-cells, but produced in a similar way to the five exterior empty cells in *Nigella*.

another, by the outer surfaces which are in contact. Thus is formed an apparently simple but many-membered pistil (*p. simplex, polymerum*). This coherence may extend to the entire pistil, as in *Apocynaceæ;* or it may only extend to the germen and style; or only to the germen itself; from which may proceed either a simple germen, with a simple style and several stigmas (as in *Geraniaceæ*), or no styles but several stigmas (as in *Phytolacca*), or a simple germen with several pistils and several stigmas (as in *Buxus*). It is very unusual for the germens and pistils to remain separated, and only the stigmas to be coherent; but this occurs in the *Asclepiadaceæ*. In all these cases, the germen is called many-celled (*plurilocularis*). The cells (*locula*) are divided by septa (*dissepimenta*), which, by reason of their origin, are double, and of course alternate with the carpels, and, consequently, with the stigmas. Occasionally the production of false partitions occurs here by the growth inward of cellular tissue, as in the *Labiatæ* and *Boraginaceæ*, where the really two-celled germen becomes spuriously four-celled by means of such spurious dissepiments.

*b.* Or the carpels may become united together by their edges, so that they form a simple, many-membered germen, a style with a simple tube, and a simple or multifold stigma (*p. simplex, polymerum*). This pistil has, however, here only one cell like the one-membered (*uniloculare*). Spurious dissepiments seldom exist here; these generally, perhaps exclusively, originate in a peculiar development of the spermophore, as in the *Cruciferæ*, in which the course of development is easy to follow.

II. *Of the false inferior Germen.* — With the formation of a concave disc, it sometimes occurs that the several simple, monomerous, superior germens which it surrounds, become not only blended together, but with the disc, and so present one uniform mass, which supports the remaining parts of the flower, and from which the styles and stigmas project to greater or less extent. This occurs in the *Pomeæ*, where only one circle of germens exists, and in the *Granateæ*, where two circles stand together. This structure is altogether different from the true inferior germen. In the former the individual germens are formed from foliar organs, and blended with the axial organ; but in the latter it is a true form of the axis which exclusively constitutes the germen.

III. *Of the inferior Germen.* — In a large number of families, the collective internodes from the calyx to the carpels expand into a hollow, cup-shaped, or even tubular body, which bears upon its borders all the rest of the floral parts, and on its inner surface developes the seed-buds, and thus becomes the germen. The carpels, when they are blended with one another at their edges, form only the upper covering of the cavity of the germen — the style, when it is present, — and with their free extremities they form the stigmas. But their share in the formation of the germen varies greatly. If

the inferior germen is only a shallow excavation, as in *Saxifragaceæ* and *Myrtaceæ*, the part which the foliar organs play in the formation of the cavity is very important (*germen semiinferum*); if the germen is already, by the form of the internodes, closed at the upper part, as in the *Onagraceæ*, then they only form the styles and the stigmas. If, however, as not unfrequently happens, the tube formed of the internodes is elongated above the floral envelopes, a false style is produced, formed from the internodes, which then commonly bears the stamens; and the carpels remain only as small scales, forming the stigma; or they are entirely wanting. This is the structure in the *Orchidaceæ* and *Aristolochiaceæ*; and it is strikingly exhibited in the *Stylidiaceæ*. In these germens no false dissepiments can be naturally formed; but the spermophore frequently forms false septa, and indeed, I believe, with few exceptions, opposite to the carpels, and therefore to the stigmas.

IV. *Of the superior Stem-germen.*—In *Passiflora* the superior germen originates from a cup-shaped axis, at whose edges the carpels arise, which form styles and stigma.

V. *Of the Stem-pistil.*—In the *Leguminosæ* and *Liliaceæ*, and perhaps in some other families, the extremity of the axis within the other floral parts is gradually developed to one or more flat leaf-like stems. These contribute to the formation of a pistil exactly like true leaves. The seed-buds are formed on the incurved borders below, whilst the upper part is gradually developed to styles and stigmas.

In the foregoing exposition of the origin of the germen, two essential points must be dwelt upon. The first is the formation of it from very different parts. It is around this subject particularly that the morphology of plants has hitherto groped in complete darkness, and it could do no other while men were content to labour upon the detail, without any principle of investigation to ensure certain results. The history of development can alone be our guide here, and will lead us to infallible conclusions so soon as it is generally recognised in its true light. Here I have, of course, been able to give but a small contribution, since a whole science is beyond the power of any individual, much more mine. Of anterior labours on this point, I found none; and much, an infinite amount, still remains to be investigated. The following axioms form the ground-work here: A normal bud and a leaf never originate regularly on or out of a leaf in the *Phanerogamia*, but from an axial structure; where, therefore, normal buds or leaves originate, the foundation from which they arise must be an axial organ. An organ which, from its first origin, is single and undivided, can only be explained as a combination of many parts by visionary speculation, not by healthy inquiry into nature. Undoubted axial organs occur in the so-called foliaceous form (e.g., *Phyllanthus*), bearing buds upon their margins. Undoubted axial organs form flat laminæ, concave laminæ, and even long, hollow, flask-shaped forms, almost closed at the summit (e.g., *Ficus*). If, then, we examine the inferior germens of *Iridaceæ*, *Onagraceæ*, *Compositæ*, &c. in course of formation, we always find that the cavity of the germen is

formed simultaneously with, often even earlier than, the outer envelopes of the flower, that in the border of the most distinctly formed germen originate by degrees the succeeding envelopes, stamens, and carpels; that the last, in particular, are frequently not formed until the germen is quite perfect, and even the seed-buds present in it in a rudimentary condition. For those, therefore, who have traced but a few developments in nature, there can be no doubt here, that the entire inferior germen is developed from a cup-shaped axis. In exactly the same manner, any one may attain conviction that the style, in the true *Gynandria*, the *Orchidaceæ*, *Aristolochiaceæ*, and *Stylidiaceæ*, is equally an axial structure. For if it be recalled to mind that in the disc and cup-shaped axes, the upper or inner surface is the organically higher part, and the centre of the disc the highest point of the axis, it becomes easy to refer those abnormal phenomena to well-known and commonplace structures. In the *Onagraceæ*, for instance (fig. 216.), the entire outer surface of the cavity of the germen (*a*—*b*), and the so-called tube of the calyx up to the free lobes (*b*—*c*), correspond to the pedicel: next follow the internodes between calyx and stamens, which are not elongated; the inner surface of the so-called tube of the calyx up to the style corresponds to the internode between stamens and carpels, which is elongated, as in some degree in *Cleome:* lastly, the inner surface of the cavity of the germen corresponds to an elongated axial structure contained within the carpels, therefore to the so-called *spermophorum centrale liberum.* In *Orchis* (fig. 217.), *Aristolochia*, and *Stylidium*, the external surface

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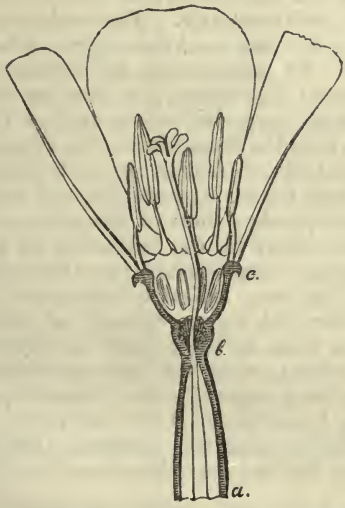


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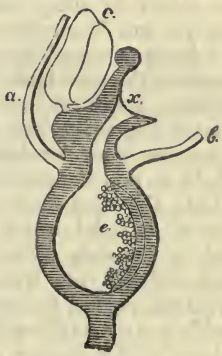


* See Plate III. figs. 18—22., with the explanation.

[216] *Godetia Lehmanniana.* Longitudinal section of the flower. The shaded portion is the axial organ, and from *a* to *b* the inferior germen (fig. 215.); from *b* to *c*, the superior cup-shaped disc (fig. 211.). This superior disc exhibits projections and ornamental markings, which are developed exactly in the same way, only in a less degree, as on the inferior disc of *Passiflora.* (See Plate IV.)

[217] *Epipactis latifolia.* Longitudinal section of the flower. *a*, Outer, *b*, inner peri-

of the germinal cavity corresponds to the pedicel; the border of it is the undeveloped internode between the inner and outer circles of floral envelopes in *Orchis* and *Stylidium* (in *Aristolochia* only one circle exists). The outer surface of the hollow columella corresponds, in all these, to the developed internode between the inner floral envelopes and the stamen, such as occurs, for instance, in *Passiflora;* the border of the columella is the undeveloped internode between stamens and carpels, and the inner surface of the columella is the lower part destitute of seed-buds, of the central spermophore, as it occurs in some measure in the *Primulaceæ.* In the same way the history of development leads to the conclusion that the germen of *Passiflora* is a stem-organ, since the cavity of the germen is indicated before the stamens show themselves, and exists, distinctly formed, before the appearance of the carpels. (See Plate IV., with the explanation.)

Less easy and certain is the decision of the question of the origin of the stem-pistil; especially difficult must it be to become accustomed to regard it in this point of view, to those who are still trammelled by the common prejudice set up without any investigation, and therefore wholly unfounded, that every pistil must be formed of *carpels.* When a conviction has been arrived at of the correctness of the preceding exposition, and it is seen that even here, in the inferior germen, the most essential part, the germen, is always, and the style often, formed out of axial organs, the notion will be more readily accepted that the superior pistil may also possibly be wholly composed of axial organs. The following axioms will serve as a point of departure: Axis and leaf are not distinguishable by any difference of external form, but by their peculiar process of development; in the leaf the apex is formed first, the base last; in the axis the contrary is the universal rule. That which *regularly* produces normal buds is not a leaf but an axial organ. Observation gives us the following facts: In some pistils, for instance, in *Cruciferæ* and *Fumariaceæ* *, the stigma is perfected first, then the style, next the germen, and last of all in this, on special organs distinct from the carpels, the seed-buds; in others, as in the *Leguminosæ*, the *Liliaceæ*, the germen is formed first, and in this the seed-buds, on the borders of the plates, appearing like carpels; then the style grows up; and at the very last the apex developes into the peculiar form of the stigma. If we apply to this the criterion which we have for the distinction of stem and leaf, the first mode of development corresponds to a foliar, and the last to an axial, organ; and so long as a logical consistency is regarded as the only means to maintain the secure advance of science against mere playing with words, we must, in the present condition of observation, regard the pistils in question as formed from axial organs. Probably very many families belong here, especially the *Ranunculaceæ*, on which, in the absence of complete investigation, I will not venture to judge. The most interesting deviation from the structure, hitherto regarded as normal, occurs in a plant, *Siphonodon celastrineus*, described

* Especially adapted, on account of their remarkably formed stigma.

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anthial leaves (half removed); *c*, stamens; *e*, seed-buds; *x*, stigma. The shaded portion is the axial organ, and up to the point of junction of *a* and *b* constitutes the inferior germen: above this, at first an androphore, then a gynophore. The carpels, however, are wholly abortive; and the axial organ itself forms the style, with the two last-named parts above *a* and *b*.

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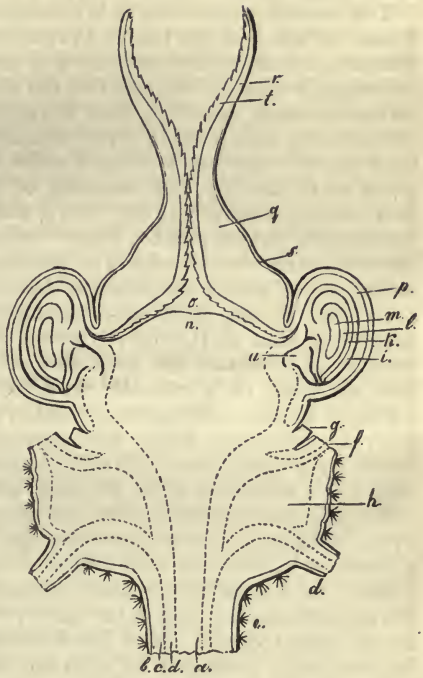



by Griffith.* I think one may obtain the clearest idea of the pistil of this plant † by imagining the pistil of a Malvaceous plant, e. g., *Lavatera* (fig. 218.), with the whole of the stigmas (*q*) abbreviated to little teeth, and the conical extremity of the axis elongated like a pedicel beyond the stigmas, and then spreading out like an umbrella. Here the carpels form the germen and tube of the style, while the axis is at once central spermophore, conducting tissue and stigma.

The result of all these discussions is that the germen, style, and stigma are by no means definite fundamental organs of the plant, but different modes of appearance, sometimes of the axial, sometimes of the foliar, organs. But the said parts are decidedly inessential portions of the flower, since they may be wholly absent, and therefore there is no thorough unity to be looked for here. On the other hand, the properly essential organs of the flower are different as fundamental organs. The stamens are always (only in *Najas* it is still doubtful) foliar organs; the seed-bud, and the part on which it is borne, the spermophore, also constantly axial organs. The whole terminology must therefore really be reconstructed, since germen, style, and stigma, as definite organs, must be excluded. If we name every exclusively axial organ which bears seed-buds spermophore, — in plants with inferior germens no germen exists, but merely a cup-shaped spermophore, a style and stigma perhaps, or merely a stigma; in the plants with a stem-pistil there is nothing but a false pistil, that is, a spermophore in the form of a pistil. We shall hereafter find the scales of the *Abietineæ* to be analogues of these. It is also easy to see, that in a complete carrying out of such

* Calcutta Journal of Nat. Hist. vol. iv. p. 150, et seq.

† I only know the description, and have not seen the figures given by Griffith.

218 *Lavatera sanvitellensis.* Longitudinal section of the flower. *a*, Pith; *b*, epidermis; *c*, cortical layer; *d*, vascular bundle of the pedicel (*e*); *d*, *f*, *g*, remains of the removed epicalyx, calyx, corolla, and stamens; *h*, peculiar spongy cellular tissue of the receptacle; *i*, *k*, *l*, *m*, external and internal integument, nucleus, and embryo-sac of the seed-bud; *n*, flat hemispherical extremity of the axis in the flower; *p*, lower, *q*, intermediate, *r*, upper part of the carpels, forming the cavity of the germen, style, and stigmas; *s*, conducting tissue, on which the pollen tube passes down into the common space (*o*), from whence it penetrates into the separate cells of the germen, right and left of the spermophore, which is here an immediate prolongation of the axis.

investigations through all parts of the flower, many at present doubtful * alliances of the families of plants will take a very different order; many certain ones be more accurately established and expressed.

The second point which it is here essential to make good, and the influence of which in the theory of reproduction is of the most decided importance, relates to the connection of the cavity of the germen with the external air through the canal of the style. That any one has opinions on reproduction, deserving even the slightest attention, nay, that any one can institute researches into reproduction with a hope of any useful result, who has not previously become quite clear in this point, is to me as plain, as in Zoology, the necessity of the previous inquiry whether a free passage exists between ovary and uterus, and between these and the external sexual parts. That "*laisser-faire*" folks, who on this point have not even once attempted to establish their opinions through original investigation, should undertake to discuss the theory of reproduction, and even to set up new theories, — persons who are at the same time skilful observers, such as Hartig *, — proves how sad the condition of science actually is, how little the generality of men have yet comprehended the true character of a scientific examination of organic bodies. That this reproach applies to botanists generally, and not to individuals, is evident from the acceptance which such essays meet with. If a zoologist were to set up a new theory of reproduction, and in it to assert that the uterus is a sac closed in on all sides, all zoologists would laugh and cast the treatise aside without further notice. Botanists in general have not even advanced so far as to see how indispensible the settlement of such a question is, and thus such treatises circulate, are copied, half-comprehended, used as materials from whence to spin out new fantasies, and the science remains ever at the same low point, around which it revolves in an eternal circle. Men like Robert Brown, Mirbel, Brongniart and Meyen, write altogether for oblivion, because they find no public which is capable of estimating their labours; since a man may talk well about many things, but has a scientific judgment only on such objects as he is acquainted with through his own researches; and how many among the hundreds of German botanists may there be, who have even once attempted to form an independent opinion of the nature of the organs of propagation of plants by the investigation of their development on only one single plant? Would it, in these days, be forgiven a zoologist not to have himself once made the *complete* course of development of a chicken, or some other animal, an object of his investigation? — a subject which is so difficult, that the history of development of a germen appears as mere child's play beside it.

When the formation of any germen whatsoever is traced, it is seen in every case, from whatever fundamental organs it may have originated, that the cavity of the germen is always open to the external air, either immediately, if only a stigma (*stigma sessile*) exist, or through the canal of the style, which is indeed merely a prolongation of the cavity of the germen; since the parts from which the pistil is produced are always formed as flat structures. In monomerous pistils, the margins become applied together and blended, from below upward, so as to form a continuous tube, open above; in pistils composed of a number of parts, these

* How little is as yet certain in this respect is shown by every new systematic work that appears: every one throws the families together in a different way, into a self-styled thoroughly Natural system.

† New Theory of Impregnation, &c. Brunswick, 1842, p. 7.

become applied together and blended at their margins, forming, in like manner, a tube open at the summit; in both cases the lower part of the cavity of the germen usually begins to enlarge at a subsequent period. In inferior germens the carpels form, in the same way, a tube* communicating with the cavity of the germen. With the exception of the *Asclepiadaceæ* and *Apocynaceæ*, there is probably not one single family in which the original canal of the style and the orifice at the stigma becomes actually grown up; in most, this canal may be seen in the perfect pistil as a tube, with a not inconsiderable cavity, and traced into the cavity of the germen. In the others, no such empty space containing only air can of course be distinguished; but it nevertheless exists, and is merely rendered indistinct by a peculiar modification of the cellular tissue which lines it, of which I shall have to speak hereafter. As I have said, I know of no exception. Most Monocotyledons which I have examined have an entirely open tube in the style; among the Dicotyledons, e. g. in *Viola*, *Euphorbia*, *Ricinus*, *Phytolacca*, most *Malvaceæ*, *Cruciferæ*, it is the same. In the *Orchidaceæ*, the tube, which is open and proportionately very wide before the germen is perfect, certainly appears closed at the epoch of flowering; but it is not so in fact. Even in the *Proteaceæ*, to which, I think, Treviranus even denied a stigmatic surface, the canal may be clearly demonstrated.

In conclusion, I will add a few observations on some less essential modifications in the form of the pistil and its parts. All here turns upon the point which I have placed at the threshold of the whole subject of Morphology, that the dimensions never determine the definition of an organ: that, therefore, the said three parts of the pistil may occur filiform, flattened, thickened, or globular (capitate), is self-evident. Thence, globular (capitate), leaf-like, flat (and then with entire or variously divided borders), or funnel-shaped, filiform, &c. stigmas, are almost equally frequent; the style is of course usually filiform, but in the *Malvaceæ*, for example, conical†, in *Iris* and *Canna* petaloid. The forms of the cavity of the germen are infinitely varied; generally, however, globular, ovate, or longish. One peculiar form may be briefly mentioned. When a many-membered pistil is closed up at an early period and the germens, chiefly at the lower parts, and this toward one side, expand, this portion advances, bulging over the point of departure of the style, so that the latter appears to arise, not from the summit but from the side, or even from the base of the germen; where several blended carpels have been developed in this way, the style appears to arise between them from the receptacle: this is called a *stylus gynobasicus*, which however, is not distinguished in any respect from the *stylus lateralis* and *basilaris* of some *Ranunculaceæ* and *Rosaceæ*.

* I will here, in passing, remark that the style is *never* a continuation of the mathematical axis of the flower, as Link says (El. Phil. Bot. ed. 2. p. 217.), but always a prolongation of the wall of the cavity of the germen proceeding out from it. The investigation of *every* course of development of the germen proves the contrary. Just as little does any process of the axis exist in the *Geraniaceæ* (Link, ibid.): the five germens originate at once, separate and free, and become blended together; *no* other organ whatever appears among them. A hundred similar observations might be made, since the old ones have done their best to leave the younger the whole harvest of discovery undiminished, without our acquiring a right to be proud of our skill. We do now what should have been done long ago,—we look into things instead of making words.

† A childish game at making words has here invented the superfluous name of *modiolus* for the style.

The structure of some *Malvaceæ* also deserves remark (*Malva*, *Althæa*, *Lavatera* (fig. 218.), *Malope*, &c.). Here the axis of the flower forms a conical or flat hemispherical body (fig. 218. *n.*) (*gynophorum*) in the middle of it, on which a whorl of carpels (fig. 218. *q*) is produced in (in most) a simple circle, or tortuously alternating up and down (*Malope*), in the axils of which one or two seed-buds are developed (fig. 218. *i k l m.*) The carpels with their lower parts (218. *p*) embrace the seed-buds on the outside and laterally, and are blended together so far by the outer surfaces of their *incurved* borders; a higher part of the carpels (fig. 218. from the seed-bud to *s o*) (growing together in the same way) forms a half canal, the lower open side of which rests upon the spermophore; lastly, in the upper portion, the carpels become partially blended together by their borders, and thus form *one* canal of the style (fig. 218. from *s* to a little below *t*), and remain partly free, forming the stigmas (fig. 218. *t.*) Here then is a perfectly free communication from the exterior to the seed-buds, which is scarcely anywhere so easy to trace as here. It is inconceivable to me how Hartig can say, "There are cases in which the ovules do not lie in the interior of the canal of the style enlarged into a seminal cavity, but are perfectly closed up by masses of cells, in which, in some measure, a *parietas* (?!!) *extrauterina* takes place, as in the *Malvaceæ*, the *Cruciferæ*, *Campanulaceæ*, and many other plants, in which no connection of the ovarian cavity with the stigma by special conducting tissue ever exists." In the *Campanulaceæ* and *Cruciferæ* even, it is certainly anything but difficult to trace the canal from the stigma to the cavity of the germen; but in the *Malvaceæ* Hartig *must* know, that he has either not investigated the matter at all, or in the most superficial manner possible.

Symmetrical forms also occur in the pistil, although more rarely than in the floral envelopes. Thus, the germens on the spadix of *Cryptocoryne spiralis* are formed so obliquely, that almost the whole circumference is formed on one side only; and the stigmas, instead of lying opposite the base, are pressed quite close to the spadix, which give rise to a completely false idea of the condition of organisation. Other examples are afforded by the *Scrophulariaceæ* and allied families, &c. A strange, hitherto unmentioned form of the germen is exhibited by *Celosia;* here, when the long style is cut away, the germen has exactly the form of a perfect *Agaric;* the stipe contains the funiculi of the (numerous) seed-buds, the pileus the seed-buds themselves.

§ 159. The structure of the pistil differs with the different modes of its origin, and still more in reference to specific peculiarities. Like every newly-formed part of a plant, it consists originally of uniform, delicate parenchyma, in which an epithelium on both the outer and inner surfaces is distinguishable. Gradually, but sometimes not till a late period, or in certain cases not at all, the vascular bundles are organised from the parenchyma; in the single carpel there is usually one main bundle, corresponding with the central rib of the leaf, and two others at the edges of the leaf; in many-membered one-celled germens, the latter are frequently wanting. In rare cases the vascular bundles are ramified in the same way as in the leaf, which indeed is the natural consequence of their morphological import, since germen and style correspond to the vagina and petioles, which are generally traversed by only one, or a

few parallel vascular bundles. The stigma, on the other hand, corresponds to the lamina, and is so imperfectly developed that in most instances it contains no vascular bundles. In a few cases interesting modifications of cellular tissue are presented in the interior of the germen; yet oil-passages (*Umbelliferæ*), milk-vessels, and cells containing crystals, &c., occur here and there. The external epithelium of the outer surface is commonly soon changed into epidermis, which often exhibits stomates, and under this the parenchyma is somewhat lax and almost spongy. The surface of the germen exhibits all the various appendages of young epidermis, hairs, prickles, glands, &c. The style is sometimes clothed with hairs, which are termed collecting hairs (*pili collectores*), because the pollen remains attached to them. The peculiar hairs upon the styles of some of the *Campanulaceæ* are worthy of attention; they have already been spoken of (§ 29.). They have served as the basis for many fanciful notions. The formation of the epithelium of the inner surface is more important; it is sometimes developed with the next subsequent layers into a true epidermis, but only in the cavity of the germen (rarely, as in *Passiflora* and some *Cruciferæ*, furnished with stomata). On the stigma it is converted, either partially or entirely, into papillæ, as it also is sometimes in the canal of the style, if this is distinctly hollow, and in the cavity of the germen along the spermophores, as far as the seed-buds, where the papillæ frequently become long hairs. All these papillæ commonly secrete at the time of the perfecting of the pistils an adhesive substance, containing gum or sugar, the stigmatic fluid. A similar substance is frequently secreted in the intercellular spaces of the cellular layers lying immediately beneath the epithelium of the stigma and the styles, and often so copiously that the cells are loosened from their union with one another, and lie loosely imbedded in this mucilaginous, semi-fluid matter. The process may be easily followed in the *Orchidaceæ* and the *Onagraceæ*. The epithelium generally, so soon as it becomes papillose, together with all the cellular tissue and the secreted matter, is termed conducting cellular tissue (*tela conductrix, conductor fructificationis*, Horkel; *tissu conducteur*, Brongniart). In rare cases, in the *Asclepiadaceæ* and *Apocynaceæ*, where the upper opening of the canal of the style is perfectly closed, a conducting cellular tissue of this kind is formed through the thickness of the wall to the outer surface. In the *Asclepiadaceæ* a peculiar secretion is presented at the five angles of the great body formed by the blending of the stigmas, from which proceed five glandular, scarcely organised structures, each with two arms, coated with viscine, and, as has already been noticed, receive the pollen masses at the time of the dehiscence of the anthers.

Of the last-mentioned matters, the structure of the conducting cellular tissue only is of essential importance. But this again gives striking evidence of how vague and obscure all investigations and so-called theories remain, when they are not based on the history of development. Brong-

niart long since mentioned, that in several plants the stigma is clothed by a structureless pellicle (*cuticula*), as, for instance, in *Nuphar*, *Nyctago*, and *Hibiscus*. Here he erred on account of examining the stigmas too late, after the secreted viscid matter had become solidified: at the time when the flower opens this imaginary pellicle is a thickish and amorphous fluid. In most plants, however, Brongniart had recognised the real nature of it, although he had not observed its gradual formation as a secretion from the neighbouring cells. Quite recently, Hartig has, from the most imperfect observation of this substance, built up a comprehensive so-called theory, including not merely impregnation, but even cell-formation, which, in reality, contains nothing but imperfect observations, and these inaccurately interpreted. His whole edifice, built on such weak foundations, falls in, the moment one carefully traces the development of one single germen and its parts.

The fluid which here becomes so important, is really nothing but the intercellular substance treated of in an earlier part of this work, which is only distinguished here by being much more watery, and, as it dries slowly, remaining longer in the fluid condition in which it is secreted. If, for example, the stigmatic papillæ be observed in a perfect bud of *Iris florentina*, these are found to be longish, very delicate cells, the contents of the usual kind, with some starch granules actively circulating in currents distributed over the walls. Alcohol and acids coagulate the contents, as in all fresh, vegetating cells, and, as in all cells containing much mucus, the contents of the cells contract into the middle of the cell in a tubular form; no internal membrane can be spoken of here.* In the opening flower we find a slight secretion of mucilaginous fluid upon the apex of the papilla; this gradually increases till it forms a little cap, completely enclosing the apex, and by degrees extending down until it entirely covers the papilla: this is Hartig's external membrane. If the papillæ are not much developed, as in the plants named by Brongniart, the secretions of the separate cells flow together, and then thus form an unorganised layer on the surface of the stigma; and even over the whole wall of the canal of the style. This is the *cuticula* of Brongniart and Hartig, which, however, is in the earliest stage a tough, adhesive fluid, which may be drawn out in threads, and no membrane; and may be distinctly recognised as a secretion by its origin. In all essential points it is identical with the secretion of the epidermis, and is only distinguished, apparently, by its chemical composition, since it contains more gum and sugar, while that presents more of gelatine, and often wax and resin. It is also very different in chemical nature in different

* Hartig assumes that there are three membranes to the stigmatic papillæ. Of the outer I will speak presently; the intermediate one is the true cell-membrane, but the internal does not exist at all, and is only the appearance above mentioned. In his "Lehrbuch der Pflanzenkunde, Heft. 4.," Hartig has applied this perverse notion also to the epidermis of plants; but, from more complete ignorance of the course of development, made still greater confusion. I have already remarked on the point, that in gelatinous thickening-layers, deposited gradually in the interior of the cell, the innermost is often less soluble than the rest, and, indeed, quite naturally, from the same reason as the outer layer of the starch granule is less soluble than the inner, because the matters contained in the cell, wax, albumen, &c., impregnate this layer, with which they are always in contact. In the cases of the epidermal cell brought forward by Hartig, the outer membrane is the actually original cell-membrane; all the rest are subsequently deposited layers of increment, of which the innermost is merely less soluble on account of the matters which have penetrated it, and naturally behaves in a different way from the rest to solvents and reagents.

plants; often quite a thin fluid, as, for instance, in the *Lemnaceæ*, where it appears to be little more than a concentrated solution of oxalate of lime (?) with a little gum and sugar; it is thickest and most tenacious (and probably contains gelatine) in *Nuphar*, where it very quickly dries up into a thick and very tough membrane. When the secretion is not confined to the surface, but extends to the intercellular passages and spaces of the nearest layers of cells, the secreted substance seems to be always identical. Through this secretion the individual cells, which in the first instance form a solid tissue, become completely isolated from each other.

These cells* lying beneath the epidermis are usually of a long spindle-shape (e. g. *Orchidaceæ*, *Onagraceæ*), and about four or five times as broad as the pollen-tubes, hereafter to be spoken of. In the *Cucurbitaceæ*, they are very little roundish cells; in the *Campanulaceæ* and some others, rather long, but seldom exceed half a French line, and are always distinguishable from the pollen-tubes by their twice or three times greater diameter. They have been sometimes called mucous tubes, because, by imperfect observations, they have been confounded with the "mucous tubes" of Robert Brown, to be mentioned hereafter, with which they have nothing to do.

Some of the more remarkable forms of the conducting tissue have received special names, which are in the highest degree superfluous. Thus, in the *Plumbagineæ*, a little cord of such tissue, which has been called an *embolus*, extends from the internal orifice of the canal of the style to the exostome, lying close beneath. In *Linum*, *Euphorbia*, and *Ricinus*, the papillæ of this tissue are very long and capillary, and extend in a close body over the exostome and into it. They are of a splendid red colour near this in *Ricinus*. Mirbel first represented them (as well as the *embolus* just spoken of) in *Euphorbia*, much too stiffly and twisted like a solid body, which he called an *éteignoir*. Similar tissue of a beautiful golden yellow occurs in *Phytolacca*, and in almost all the *Portulaceæ* the micropyle is densely covered up by long, capillary, conducting cellular tissue.

I will describe rather more fully the most wonderful structure of the *Asclepiadaceæ* and *Apocynaceæ*, which has ever been a *crux botanophilorum*, and in which no one has given any useful observations but Robert Brown,† because he was the only one who looked into the mode of the formation of the parts. I have industriously investigated all the plants of this kind that I could obtain, but can, at most, only add in little detail points to Robert Brown's excellent essay. In the rudiment of the flower originate two little foliaceous (?) organs, which curve towards each other, and each separately has its margins blended, so that they form two straight tubes. In most *Apocynaceæ* they grow together at a very early period; in few, as in *Apocynum*, they remain free in the lower part. The upper part, on the contrary, which soon becomes thickened and fleshy, and soon greatly exceeds the lower part in volume, becomes blended into one in both families, so perfectly that at a later epoch the

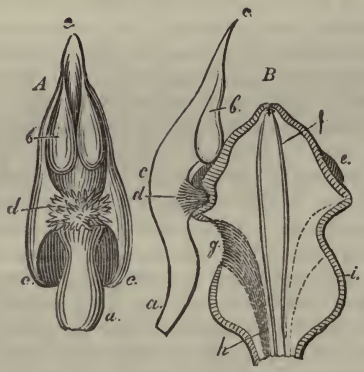
* The epithelial cells are mostly of different form from those lying beneath them, and may be distinctly made out in the earlier stages. By the solution of the cells, the epithelial cells are also scattered through the mucilaginous fluid, and can only be discovered singly with some difficulty.

† How, after Robert Brown's researches, any one can bring forward such clumsy ideas, in the spirit of the last century, as Link (l. c. vol. ii. p. 231.), is truly only explicable in *one* way, that the profound study of foreign researches does not yet lie in the spirit of our Botany.

former line of demarcation cannot be defined in the homogeneous tissue, While the lower part is thus gradually developed into the germen and a short style, while the spermophore and seed-buds are perfected, a peculiar change takes place in the upper part; the originally open canal grows up completely without leaving a trace in the interior.* The whole body acquires the specific form, which in the *Apocynaceæ* is usually a short cylinder, running up into a cone above; in the *Asclepiadaceæ* commonly a short pentagonal prism, also ending in a cone at the top.

1. In the *Apocynaceæ* (fig. 219) there is produced, on or somewhat beyond the lower or upper edge of the cylinder, a membranous, longer (*Vinca*) or shorter (*Apocynum*, fig. 219.) projecting, often wavingly-toothed (*Cer-*

219

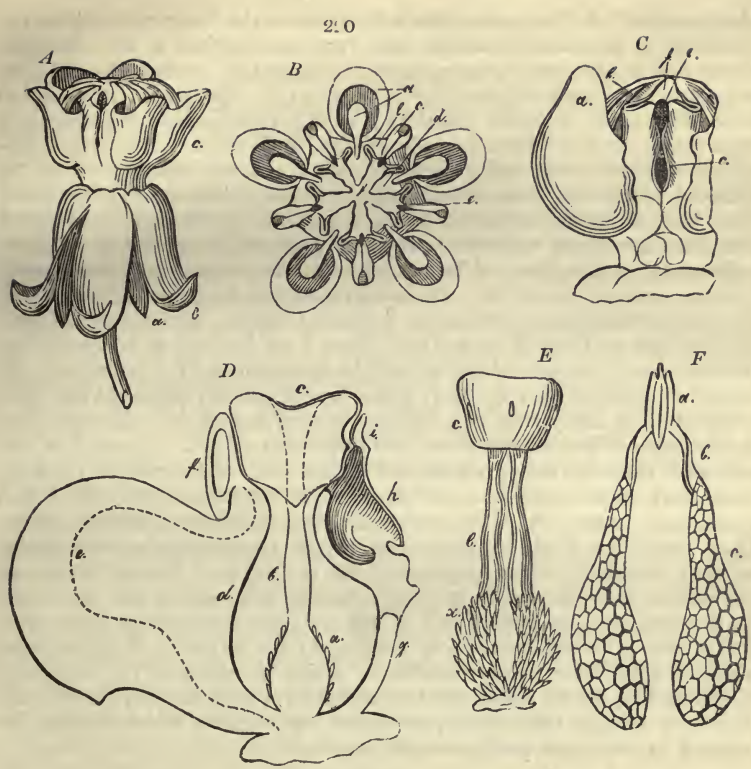



*bera*) border; above this border, or in the indentations of it, or on peculiar tufts of hair, according to specific differences, begins then the secretion of viscine, through which the tufts of hair and projections on the filaments and the bases of the anthers become firmly glued to the stigmatic body. Over the whole body a distinct epidermis has been gradually perfected, excepting close beneath the border (or in *Vinca* just above it?). Here, on the other hand, begins the secretion of the stigmatic fluid (*g*), and this is produced in curved streaks through the whole thickness of the stigmatic body (*g*, *h*), as far as the cavity of the style, and so forms a conducting cellular tissue, which breaks through the original carpel (?) and thus reaches the cavity of the germen.

2. In the *Asclepiadaceæ* (fig. 220.) a pretty thick epidermis is likewise formed over the entire stigmatic body. At its five angles it assumes a

* Two point-like excavations are frequently seen on the upper surface, traces of the confluent canal, e. g. in the *Stapeliæ*.

219 *Apocynum androsæmifolium.* *A*, Stamen, seen on the inside: *a*, filament; *b*, cell of anther; *c c c*, connective, elongated into a point above, expanded into a kind of mantle at the sides and below; *d*, tuft of hairs, between which the viscine is secreted by which the stamen becomes glued to the stigmatic body. *B*, A longitudinal section through the stigmatic body and a stamen: *a*, filament; *b*, anther; *c*, connective; *d*, tuft of hair adhering to the stigmatic body; *e*, glandular corpuscle, which lies on the distinct epidermis (*i*) of the stigmatic body; *f*, vascular bundle, on the outer side of which ran the original (now obliterated) canal of the style; *g*, *h*, conducting cellular tissue, which has been formed from the original canal of the style (from *h* downward), out through the thickness of the carpel (from *h* upward), and at *g* constitutes a stigmatic surface.




peculiar form, the cells elongating very much perpendicularly to the surface (the same occurs at five points above the border in *Apocynum*). Immediately beneath these five places five points remain without acquiring a perfect epidermis, while five cords of conducting tissue are formed from them into the canal of the style, in the same way as in the

220 *A, B, C. Asclepias syriaca. A,* Completely expanded flower: *a,* sepals; *b,* petals; *c,* stamens. *B,* The same seen from above: *a,* hood-like appendages on the back of the anther; *b,* wing-like appendages of the anther, which, retracted, form a kind of little box; *d,* crest-like elongation of the anther, which lies fast upon the stigmatic body (*f*); *e,* gland-like bodies, which, five in number, alternate with the five stamens, and adhere to the epidermis of the stigmatic body. *C,* Part of the organs of propagation from a very small bud: *a,* hood; *b,* spur projecting from it; *c, e, f,* as before.

220 *D, E, F. Gomphocarpus fruticosus A,* Longitudinal section through the organs of propagation of a very young bud: the section goes between the two germens, and on the right side between two stamens, and divides in half the stigmatic body above a stamen on the left, and on the right the tubes formed by the confluent filaments. *a,* Germen; *b,* style; *c,* half the stigmatic body; *d,* filament of the divided stamen; *e,* vascular bundle of the same; *f,* half an anther; *g,* divided staminal tube; *h,* wing-like appendage of the anther, so far as it forms the box-like body; *i,* half the gland-like body lying in the dense epidermis, which is remarkably thickened below it, and appearing as an immediate prolongation upward of the wing-like appendage of the anther. *E,* The pistil extracted free: *a,* two germens; *b,* two styles; *c,* a stigmatic body, on which three gland-like bodies are visible. *F,* Gland-like bodies (*a*), with the three arms (*b*) and the pollen-masses (*c*) appended to them, from a perfectly developed flower.

*Apocynaceæ.* In those five places lying above the five points, where the epidermis is peculiarly modified, now very soon begins, in the *Asclepiadaceæ* and in *Apocynum*, the secretion of a peculiar, viscine-like, adhesive substance, and very different forms appear; in *Apocynum* forming five little depressed, roundish cushions; in the *Asclepiadaceæ* exhibiting a rather longish body forked in the middle, and, when quite perfect, furnished with two arms going from the upper or lower end, which in the different species and genera manifest many small, inessential differences. This body is merely adherent to the subjacent, remarkably sharply and distinctly-developed epidermis; originally green, it gradually becomes yellow, and at last of a dull brown. Its structure is but very indistinctly cellular, perhaps not at all. Its origin is as yet by no means made out, for the investigation is the most difficult I know. From some original observations on *Gomphocarpus* and *Hoya*, I am inclined to conclude that the outermost borders of the wing-like appendages of the anthers are formed rudimentarily very early here, become firmly adherent and subsequently torn away from the anthers, so that each body originates from the cohesion of two fragments of two different anthers. So much is certain, that they are never organically united with the angles of the stigmatic body, for the epidermis, which was distinctly formed before their first appearance, runs on quite uniformly and uninjured, beneath them. They could, at most, in opposition to the above notion, be regarded as semi-organised secreting points. At the time of the dehiscence of the anthers they always lie in such a manner that one, mostly the upper (in the *Stapeliæ*, the lower) end of the pollen mass must at once come into contact with one arm of this body, and there adhere. Another point which I have been equally unable to decide is, whether the five cords of conducting tissue enter the two styles unequally divided (in two and three), or whether they unite just before into a circle, which is then distributed in two equal portions in the styles.

### b. *Of the Spermophore* (Placenta).

§ 160. Since the seed-bud corresponds to a bud which arises immediately from a stem, it follows that the spermophore does not always exist as a special organ: when, for instance, the axial organ from which the seed-bud springs is already defined and named on other grounds. In this case, the spermophore is nothing more than the region in which the seed-buds are attached, and, in the simplest case, this may be limited to the basilar surface of one single seed-bud; as, for example, in *Taxus*. But those places on an axial structure on which seed-buds are borne may be formed into such projecting processes that they may be well distinguished as peculiar parts of this axial organ*; or a particular part of the axis, which is in no other way defined as an organ, may be exclusively devoted to the production of seed-buds. In this way we obtain the following varieties:—

*a.* Spermophore as a simple region of another organ;

* Somewhat as in the projecting ridges on the stem of *Echinocactus* and *Melocactus*.

*b.* Spermophore as a distinguishable part of an independent organ;

*c.* Spermophore as an independent organ.

We have now to compare these with the different conditions and the various forms of the germen.

1. Where the pistil is entirely wanting, as in the *Cycadaceæ*, *Coniferæ*, and *Loranthaceæ*, we have as yet, unfortunately, so little material toward the history of the development, that we can only venture to make explanatory guesses under the guidance of laws* discovered in plants which have been well investigated. According to these the matter stands as follows:—

*a.* We find the naked seed-buds, as the immediate termination of the floral axis, without distinguishable spermophore in *Taxus*, *Ephedra*, *Podocarpus*, *Dacrydium*, and the *Loranthaceæ*.

*b.* In the axil of a bract (in *Pinus*, *Larix*, *Abies*, and *Gingko*), or without any bract (as in *Zamia*, *Araucaria*, and *Agathis*), a twig is formed which, as independent spermophore, bears the seed-bud. In *Cycas*, this spermophore is flat, and bears many seed-buds on its margins; scale-like, and bearing one (in *Agathis* and *Araucaria*), or two (in *Zamia*, *Pinus*, *Larix*, and *Abies*) seed-buds upon its upper surface; or branched like a stem, and bearing one seed-bud upon the point of each twig (as in *Gingko*).

Respecting the remaining *Coniferæ*, and especially the group of the *Cupressineæ*, for example *Juniperus*, *Cupressus*, *Thuja*, &c., I will not venture even to express a supposition, in the absence of a history of the development or sufficient analogies.

2. In the superior germens an axial organ must always project into the carpels in the spermophore.

3. In germens that are either half or wholly inferior, the floral axis itself, in the form of the inferior germen, is always the spermophore.

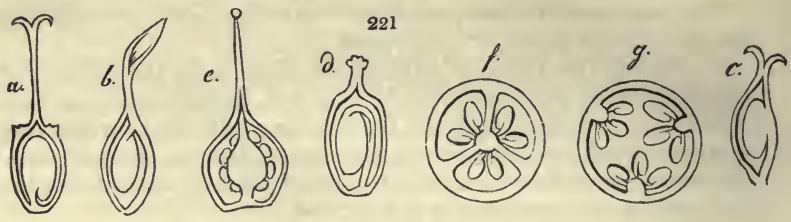
4. In the superior stem-germen and stem-pistil it is always the floral axis which bears the seed-bud. In the first, three prominent ridges are developed as spermophores; in the second, the seed-buds are formed on the edges of the flat expanded branches, curved in a little toward the interior. These edges may here form merely a slight prominence (*spermophorum parietale* of the *Leguminosæ*), or they may extend quite across the cavity, becoming blended by their meeting surfaces, so that the two seed-bud-bearing edges are placed in the inner angle of each compartment (*gemmulæ angulo loculorum interno affixæ;* as in the *Liliaceæ*).

5. Besides these cases a condition, which seems quite abnormal, sometimes occurs, in which the entire surface of the septum is covered with seed-buds; as in *Butomus*, *Hydrocharis*, *Stratiotes*, *Nymphæa*, and *Nuphar*.

These are all the varieties with which I am acquainted in the

* Of the family just named, I have as yet only followed the development of *Abies* *Taxus*, and *Viscum* so perfectly as to leave no further doubt.

formation of the spermophore. For the purposes of description they may be simply classed as follows (fig. 221.):—




*A.* A seed-bud in each germen.

*a.* Attached at the base (*gemmula basilaris*), *Compositæ.*

*b.* Suspended (*gemmula pendula*), *Typhaceæ.*

*c.* Attached to the wall (*g. lateralis*), *Gramineæ.*

*d.* Depending from a free central spermophore (*g. e spermophoro centrali libero pendula*), *Plumbaginaceæ.*

*B.* More than one seed-bud in each germen.

*e.* Attached to a free central spermophore (*g. spermophoro centrali libero affixæ*), *Primulacæ.*

*f.* Attached in an angle of the compartment of the germen (*g. angulo interno loculorum affixæ*), *Iridaceæ.*

*g.* Attached to the parietal spermophore (*g. spermophoro parietali affixæ*), *Orchidaceæ.*

There are some further general remarks to be made upon its form. The free spermophore may, like the axis, present various shapes; it may be conical, spherical, and pedicellate, cylindrical, prismatic, winged, &c. The adherent spermophore, so soon as it is to be distinguished as a projecting ridge, may be simple or split into two lamellæ, which are often very broad (as in *Begonia* and *Gesneraceæ; spermophorum bilamellatum, bifidum*); each of these lamellæ may again be divided, so that the spermophore may have four seed-bearing edges; as in *Martynia diandra.* The structure in the *Cucurbitaceæ* is peculiar; in these the parietal spermophore, extending in as far as the axis, here become split into two laminæ; these laminæ, consisting of the two spermophores applied together, turn back again to the wall of the cavity of the germen; thus a new spurious septum is formed in the compartments already formed by spurious septa, and then each curves once more to its own side in the secondary compartment, and produces the seed-buds on the free edges.

It may be originally a thin plate, the edge of which becomes thickened into a border, and this again may be angular or winged, &c. It is, moreover, by no means unusual for the substance of the spermophore to be much distended between the seed-buds, so that they are seated on, or imbedded in, little heaps of the parenchyma, as is very frequently the case in the *Primulaceæ.*

As to its structure, it is usually composed of delicate walled

cellular tissue, covered with epithelium; and only when it occurs naked (as in the *Coniferæ*), of tough, porous, woody cells, clothed with epidermis. According to its form, it is traversed by one or more vascular bundles, like a simply-formed axis; and these usually give off as many side branches as there are seed-buds present; the seed-buds may be destitute of vascular bundles, as is the case in the *Orchidaceæ*, &c. Sometimes the internal portion consists of very lax, spongy, cellular tissue, with large intercellular spaces; as in some *Cruciferæ*, *Capsella*, &c.

I will here add some few observations, and in these take the sections given in the paragraphs separately.

*Obs.* 1. Robert Brown had already shown incontestibly, from the structure of the seed-buds, that the *Coniferæ* and *Cycadaceæ* have naked seed-buds. The investigation of development, in which an integument is very easily distinguished from a germen, confirmed this truth. But this great observer had not gone beyond this, and therefore took the certainly leaflike scale for an open carpel the more readily, that at that time the view was universally received that seed-buds were formed on the borders of foliar organs. But so soon as the history of development had shown beyond doubt that, at least in a great number of plants, the seed-buds cannot have their origin from a foliar organ, but are borne immediately by the axis*, this old prejudice lost all value; and the question now arose for every single group of plants:—Is the part which bears the seed-bud an axial or a foliar organ? Whence shall we now take the ground of distinction? The following expresses the train of thought:—1. In the *regular* course of vegetation a normal bud *never* arises according to law at a definite place on a leaf: when buds arise according to law at definite places, the base is always an axis. All cases which are brought forward in opposition to this are occurrences which happen under conditions foreign to the normal vegetation of the plant, but on this alone may we build any theory. 2. Throughout the whole vegetable kingdom *no* simple leaf is *ever* formed in the axil of another leaf; that which arises in an axil is always an axial organ with more or less perfect leaves. 3. Leaf and axis cannot in any way be distinguished by external form, but only and solely by the process of development; therefore, as to the foliar or axial nature of a doubtful organ, the only means of decision, besides the 1st and 2nd analogies just mentioned, is the history of development; but this latter gives the safest conclusion.

Now, we find in *Abies* that in the *axil* of a foliar organ exists another organ, which is formed exactly like an axial organ, and subsequently has buds (seed-buds) developed upon it. This organ is consequently not a carpel but a free spermophore. Having obtained this result with certainty, we may now judge with greater confidence in the other *Coniferæ* and *Cycadaceæ*. Accordingly, the female flower of *Cycas* and *Abies* are only distinguished by the fact, that in the former the spermophore bears several unreversed seed-buds. Here it is pre-supposed that it also arises from the axil of a leaf, which, unfortunately, has not been noticed by any botanist who has had the opportunity.

* Of these, with easily traceable development, may be given *Taxus* and *Viscum*, from which we may venture to assert a similar origin of the seed-bud in *Ephedra*, *Podocarpus*, *Dacrydium*, and in the rest of the *Loranthaceæ*.

*Obs.* 2. The following cases are possible here :—

*a.* The floral axis, as terminal shoot, itself bears one seed-bud, either without being distinguishable in the cavity of the germen as a special organ (spermophore) (*gemmicula basilaris*, e. g. *Zea Mays*), or elongated into the cavity as a free central spermophore (*gemmula ex apice spermophori centralis liberi filiformis pendula*, e. g. *Statice*).

*b.* The floral axis, more or less elongated into the cavity of the germen as a central spermophore, bears the seed-buds as lateral buds (*gemmulæ angulo interno loculorum affixæ*, in part, and the *spermophorum centrale* of descriptive botany, e. g. *Ericaceæ*) ; if there are not more seed-buds than carpels, the former appear as axillary buds of the latter (e. g. *Lavatera*), otherwise they have no supporting leaves (e. g. *Labiatæ* and *Boraginaceæ*). If the borders of the carpels do not turn inward and become blended with the spermophore, the latter stands free in the midst of the cavity (*spermophorum centrale liberum*, e. g. in the *Primulaceæ*).

*c.* The floral axis is ramified in the cavity of the germen, and the shoots (axillary shoots of the carpels) curve immediately from their origin toward the side, and become blended with the margins of the two carpels on their inner side, as parietal spermophores, bearing the seed-buds as lateral buds (*spermophora parietalia*, e. g. in *Resedaceæ* and *Cruciferæ*). Here the spermophores may be so uniformly blended with the carpels as to be indistinguishable as special organs, or they may project by the seed-bud-bearing margin into the cavity, and even meet in its axis, thus forming spurious central spermophores, or, lastly, may expand as a naked lamella between the seed-buds, come in contact in the interior of the cavity, here unite with one another, and form false septa (e. g. in the *Cruciferæ*).

In the case of the superior germen, we find a great number of plants in which the immediate origin of the seed-buds, as true axial organs, follows at once from their position, and this is decisively confirmed by the history of development. I here name only the following plants*, in which I have myself observed the development, and for which I can therefore answer: *Amarantaceæ*, *Ardisiaceæ*, *Aponogeton*, *Arum*, *Ambrosinia Bassii*, *Berberaceæ*, *Cyperaceæ*, *Chenopodiaceæ*, *Caulinia*, *Calla palustris*, *Cryptocoryne spiralis*, *Caladii spec.*, *Ericaceæ*, *Globularia*, *Gramineæ*, *Illecebraceæ*, *Lemnaceæ*, *Linaceæ*, *Malvaceæ*, *Melianthus major*, *Myricaceæ*, *Najas*, *Nyctaginaceæ*, *Orontium aquaticum*, *Primulaceæ*, *Plumbaginaceæ*, *Polygonaceæ*, *Portulaceæ*, *Piperaceæ*, *Pistiaceæ*, *Polygala*, *Plantago*, *Sauromatum guttatum*, *Trapa natans*, *Urtica*, and some others presently to be mentioned. Such a series cannot certainly be explained as isolated exceptions, but allows us to conclude the existence of such a wide prevalence of a law, that, moreover, presumption does not speak in favour of the formation of the spermophore out of the border of a leaf, but against it, especially when it is remembered that many families, genera, and species allied to those named, admit of being added to them by analogy, at first sight, and with certainty, in particular *all* plants, without exception, with *spermophorum centrale liberum* or *gemmulis basilaribus*. To this may be added the plants in which the seed-bud is nothing in the world else than the axillary bud of the carpellary leaf, of which I can name the following: *Alisma*, *Dryadeæ*, *Euphor-*

* In very uniform families I have always examined several genera ; in genera, a few species.

*bia, Limnanthes Douglasii, Luzula, Malvaceæ loculis* 1-*ovulatis, Mercurialis, Phytolacca decandra, Sagittaria, Tropæolaceæ, Triglochin.* The said plants comprehend the cases named under *a.* and *b.* For the case of *c.* speaks the entire course of development in the *Cruciferæ;* in the *Resedaceæ,* however, both this and the most beautiful retrograde metamorphoses in all conceivable intermediate stages, which occur frequently enough in gardens in *Reseda alba.* A great many cases of course remain undecided, in which I can only assume the axial structure of the spermophore: on these, future investigations of the development can alone decide; hitherto my time has not been sufficient to work up more material.

Here, again, the following varieties occur; namely, the true central spermophore, blended with true septa (in *Solanaceæ, Acanthaceæ,* &c.), the spurious central spermophore formed out of the parietal spermophore, which projects in as far as the axis of the cavity of the germen, which thus becomes spuriously many-celled. The latter two cases are frequent.

In regard to the *gemmula basilaris* I will once more mention that the unilateral development of the receptacle often makes the spermophore appear like part of the wall of the cavity of the germen, which, in fact, is only the bottom of it, and that, hence, seed-buds may also be *spurie laterales,* which really are *basilares;* this is especially the case in all Grasses, Potamogetons, and perhaps in many others, of which we are at present ignorant of the course of development.

*Obs.* 3. Persons may think what they will of the nature of the inferior and half-inferior germens, but there are cases here beyond doubt, where position and course of development demonstrate the seed-bud to be an immediate prolongation of the axis. Here are included, above all, the extensive family of *Compositæ,* which, comprehending a tenth of the whole Phanerogamic vegetation, give no little weight to the idea of the universal law of the formation of the spermophore out of the axis. I will further name, from my own researches, the *Juglandaceæ, Elæagnaceæ, Lonicereæ, Rubiaceæ,* and *Peliosanthes Teta.* In none of these can any tolerably accurate observer doubt that the spermophore is an immediate prolongation of the floral axis, and itself an axial organ. The same result is obtained from the investigation of the development of the *Myrtaceæ.*

If, however, the development of an inferior germen is accurately traced, not the smallest doubt remains that this itself is also merely an axial organ; and in the parietal formation of the spermophore it is equally certain, where the carpels do not even apparently project into the cavity of the germen, that the seed-buds are seated on an axial organ. In order to comprehend the spurious central spermophore, it must be called to mind that the inner surface of a cup-shaped axial organ corresponds to its sides in the usual condition; now if these exhibit projecting ribs, on which the buds are seated, somewhat as in *Echinocactus,* in the concave shape these ribs must project inwards, and the carpels above may be blended with these projections of the axis running upwards, like the so-called *folium decurrens* with those running downwards. On the other hand, it must be recollected that these projections (which form the spurious septa and bear the seed-buds) are perpendicular from the margin of the cavity of the germen to its base: this direction, however, corresponds to that from below upwards in the usual condition of the

axis, and no leaf is ever attached to an axis in this way, but always in the transverse direction: already from this it follows that these projections cannot be leaves. Finally, if the wing of the axis in the *folium decurrens* is assumed to be a real foliar part, the analogy would be inapplicable here, since the direction, if from the margin of a hollow axis to the bottom of its cavity, corresponds to the direction from below upwards: now we really know the so-called decurrent leaves, but leaves running up a stem are unheard of. Thus the assumption of the formation of the spermophore from the axis appears to be unexceptionably established for this section. The conditions which occur may be arranged according to the following review: —

*a.* The terminal bud, therefore the innermost and lowest part of the cavity of the germen, may develope as seed-bud (*gemmula basilaris unica in germine infero*, e. g. in the *Compositæ*), or the axis may rise up again in the cavity of the germen, and bear the seed-buds as lateral buds (*spermophorum centrale in germine infero*, e. g. in the *Myrtaceæ*).

*b.* The internal surface of the cavity of the germen bears the seed-buds in as many lines as there are carpels, without further marking of the spermophores (*spermophora parietalia*).

*c.* From the internal surface of the cavity of the germen project as many ridges, in the same arrangement, the free angles of which bear the seed-buds (*spermophora parietalia*, e. g. *Orchidaceæ*).

*d.* The projecting ridges become so broad that they meet in the axis of the cavity of the germen, and thus form spurious septa; then their borders split into two layers, which, somewhat recurved, project into the two contiguous cells, and each bears seed-buds in its free angle (*gemmulæ in angulo loculorum interno affixæ*, e. g. *Iridaceæ*).

*Obs.* 4. Here I have nothing to add, but only to direct attention to what has been said regarding the germen. If I was right then, the matter here is self-evident.

*Obs.* 5. On the cases here brought forward I will not venture to judge, because I do not know the complete course of development. In an earlier work (yet trammelled by the spirit of the old school in which I learnt) I have helped myself out with analogies and guesses, which I here expressly recall. True observation and investigation of nature have shown me how this road can never lead to safe conclusions, and in most cases does lead to error, since, to use analogy, we must first have higher principles of unity and universal laws; and these are just what we as yet are destitute of, and can never be gained in the manner in which it has been attempted hitherto. Therefore, I prefer rather to confess my ignorance, where I know myself not to be warranted by a complete knowledge of the development, than to think only of the present, and purchase the distant possibility of being held an acute observer of nature, with the much closer probability of a most wretched blunder.

Finally, I have a few general remarks to subjoin. It is a frequent phenomenon for the seed-buds to be seated on two- or many-budded linear spermophores, and since in these cases just as many spermophores as carpels, therefore twice as many rows of seed-buds, exist, this condition has much contributed to nourish the prejudice that the seed-buds arise in rows from the margins of the carpels. With the countless instances of a different kind of structure of the spermophore, the correctness of this relation admitted, the matter would not be of great importance. But we have quite a different explanation afforded us of the bi-seriality of the

seed-buds, which especially prevails in the cases where the spermophore is central, or belongs to the inferior germinal cavity; if we here put out of view the metamorphosis of the fundamental organ, and continue the arrangement of the carpellary leaves in equal-membered alternating circles, we obtain, with two carpels four-ranked, with three six-ranked leaves, therefore four or six rows of axillary buds. By the conversion of the axis into the spermophore the regular rows of buds are pressed nearer together in pairs. If we examine, in this respect, *Tillandsia amœna*, we find really six spermophores, which are approximated in pairs, but neither so morphologically nor anatomically connected as to justify us in regarding them as three two-leaved organs.

Where, however, the spermophores are to be regarded as lateral branches of the floral axis, whether in germens formed of carpels or in the stem-pistil, we must always look upon them as flat shoots folded together, which then, somewhat like the flat shoots of *Phyllanthus*, bear two rows of buds.

On the structure of the spermophore I have no additional remarks to offer, since no especially striking conditions are known to me.

### c. *Of the Seed-bud* (Ovule).

§ 161. Every seed-bud (*gemmula*) appears at its first origin as a small roundish papilla at the extremity of an axis (terminal shoot) within the flower; as such it is an erect, straight seed-bud (*gemmula erecta, atropa*). It consists simply of the nucleus (*nucleus, chorion* [Malpighi], *perisperma* [Treviranus], *l'amande* [Brongniart], *tercine* [Mirbel]), without special integument (*nucleus nudus*). On this seed-bud are to be distinguished the base (when it does not gradually pass into the axis of which it forms the extremity) at the point of attachment of the seed-bud (*hilus, umbilicus*), and the apex as nuclear papilla (*mammilla nuclei, mamelon d'impregnation* [Brongn.]). The seed-bud seldom persists in this simple condition, as in the *Loranthaceæ*. It usually changes, partly by the formation of the integuments of the bud, and partly by the peculiarity of its modes of development, which may in general be termed curvatures.

At a greater or less distance beneath the apex of the seed-bud there arises simultaneously on the whole circumference a circular fold, which gradually rises over the nucleus and closes in it above, leaving only a small orifice. If this development is permanent (as in *Taxus* and the *Piperaceæ*), this envelope is termed a simple bud-integument (*integumentum simplex*); the upper opening is called the *micropyle*, and the part where the bud-integument and nucleus are confluent is called the base of the bud (*chalaza*). The point of attachment is here precisely defined, as in the former case. Below the first circular fold, of which we have spoken, a second is often formed, which encases the first as the first encases the seed-bud. The first is then styled the inner bud-integument (*integumentum primum internum, membrana interna* [Robert Brown], *tegmen* [Brongniart], *secondine* [Mirbel]). The other is the second or outer

bud-integument (*integumentum secundum externum, testa* [Robert Brown, Brongniart], *primine* [Mirbel]). Then the orifice of the outer integument is known as the exostome (*exostomium*), that of the inner as the endostome (*endostomium*). If beneath the entire seed-bud there yet remains a free, distinguishable piece of the axis, this is termed the gemmophore (*funiculus*). The seed-bud is found in this state of development in, for example, *Hydrocharideæ*, with the exception of *Stratiotes*, in many *Araceæ*, in the *Polygonaceæ*, &c.

This form of seed-bud is modified in many ways by means of the curvatures above mentioned.

1. The funiculus is much elongated, the nuclear papilla bends downwards, and thus the side either of the naked nucleus or of the simple or of the external bud-integument turned towards the funiculus, becomes gradually blended with it. In the perfect seed-bud the nuclear papilla then lies close to the point of attachment, the chalaza opposite to the point of attachment, and the line from the centre of the chalaza through the middle of the nucleus is straight. Such a seed-bud is termed reversed (*gemmula anatropa*); the adherent part of the funiculus is termed the *raphe*. This appears to be the most frequent form; it occurs in the naked nuclei * of *Hippuris* and *Rubiaceæ*, in the simple bud-integument of the *Compositæ*, in the double bud-integument of the *Liliaceæ*, &c.

If the blending of the funiculus with the bud-integument only affects the lower part of the seed-bud, so that a considerable part of the apex (the upper half) is left free, the seed-bud is said to be half reversed (*gemmula hemianatropa*), as, for instance, in *Meconostigma* and many *Araceæ*. If the funiculus is then very short and scarcely perceptible (*g. sessilis*), the seed-bud appears as if attached by the centre (*medio affixa, peltata*).

2. The two sides of the seed-bud are unequally developed; one remains almost totally at a stand-still, whilst the other is exceedingly increased, and in the perfect seed-bud constitutes almost the entire circumference of the seed-bud. The point of attachment and chalaza are here almost coincident; the nuclear papilla lies near the first, and a line drawn from the centre of the chalaza through the centre of the nucleus to the point of the nuclear papilla is a curved line; such a seed-bud is termed a curved seed-bud (*gemmula campylotropa*).

I am not acquainted with any example of this in the naked nucleus. *Datura* may be cited as an example in the simple bud-integument, and in the double bud-integument instances are offered

* Robert Brown also enumerates the *Apocynaceæ* and *Asclepiadaceæ* here. I have already said that the *Apocynaceæ* have a simple integument; but, more recently, I have convinced myself that in the *Asclepiadaceæ*, also, a very minute nucleus is enclosed in a thick integument at a very early period. In both families the nucleus is displaced by the embryo-sac long before impregnation; but the micropyle canal, which may be detected long before the flowering period, proves beyond a doubt the existence of an integument.

by many *Solaneæ*, the generality of the Grasses, the *Silenaceæ*, and the *Cruciferæ*.

3. The conjunction of the circumstances described under 1. and 2. produces a form in which exists a short raphe; hence the chalaza and point of attachment do not coincide, while at the same time one side of the seed-bud remains undeveloped, so that here also a line drawn from the chalaza through the centre of the nucleus up to the nuclear papilla is curved. This form is termed semi-curved seed-bud (*gemmula hemitropa*): as accompanying the simple bud-integument it is peculiar to the *Labiatæ* and *Boraginaceæ*, as accompanying the double bud-integument, to the *Leguminosæ*.

4. When a seed-bud is very much elongated, a curve is formed in its middle during its development, so that it appears curved in a horse-shoe form. Here the point of attachment and the chalaza coincide; the nuclear papilla and the point of attachment lie side by side. A line drawn through the middle of the nucleus is curved, but the two sides of the seed-bud are parallel and equally developed. If the seed-bud is confluent in the curvature, it is called an arched seed-bud (*gemmula camptotropa*), as in the *Potamogeton* and *Galphimia*; if it is not confluent, it is called a horse-shoe-formed seed-bud (*g. lycotropa*): according to Griesbach this occurs in many *Malpighiaceæ*.

5. In some few cases, after the formation of the seed-bud is complete, an additional bud-integument is produced, which more or less entirely envelopes the seed-bud: this is termed an *arillus* (in *Hellenia cœrulea*); it of course bears no part in the curvatures, which are complete at the period of its origin.

Malpighi, in his immortal works, laid the foundation for the study of the structure of the vegetable seed-bud; but his successors added nothing, and neither used nor understood what he had taught them. Treviranus, in his account of the development of the embryo, certainly did nothing to advance the knowledge of the structure of the seed-bud; he did not follow up that which Malpighi had done, and he overlooked that very important part of the seed-bud, the embryo-sac. It was Robert Brown who, in 1826 *, first gave the true history of an unimpregnated seed-bud in *Kingia australis*. Brongniart † gave some useful contributions. Mirbel ‡ subsequently investigated the history of the unimpregnated seed-bud, in which he gave most interesting explanations, but promulgated a totally incorrect view of the formation of the integuments, which, although long since refuted by Robert Brown and Fritsche, is set forth, *i. e.* copied, still in Link's Elem. Phil. Bot., ed. 2, vol. ii. p. 79, and even in much more recent works, easy as it is to make the observation in any Lily or Passion-flower, since nothing more is required than a simple microscope, magnifying some twenty times, and a couple of not particularly fine cross-

* King's Voyage, Appendix, "Botany." London, 1826.

† Mém. sur la Génération et le Développement de l'Embryon dans les Végétaux Phanérogames. Paris, 1827.

‡ Rech. sur la Struct. et les Dével. de l'Ovule Végét. lu à l'Acad. des Sc., Dec. 1828, et Add. aux Nouv. Recherches, &c., lu à l'Ac des Sc., Dec. 1829.

sections from a young germen. Robert Brown * was here again the first to strike out the true path, and showed, contrary to Mirbel's view, that the original nucleus of the seed-bud does not open at the apex and allow first the internal integument and then the true nucleus to grow forth (hence Mirbel's mistaken application of the numbers in his names primine and secundine), but that the inner and then the outer coat originate as circular folds on the base of the originally solid nucleus, and gradually envelope it. Fritsche's * observations did at least put the incorrectness of Mirbel's views beyond doubt, if his own idea of the mode of formation of the integuments was not wholly in accordance with the simple operations of nature.

Brown, in his first works, has assumed the continual presence of two integuments. Brongniart pointed out that seed-buds with one integument undoubtedly occur. In Robert Brown's Treatise upon the Fecundation of the *Orchidaceæ*, he called attention to the fact of the occurrence of the naked seed-bud, after Mirbel had correctly developed the most important curvatures presented by the seed-bud.

Excepting Fritsche, who at the time of his writing was in St. Petersburgh, not a single German botanist has done anything on this weighty point of our subject, not even so much as to re-examine the researches of the distinguished Frenchman and Englishman; and we find, in consequence, even up to the most recent dates, the false views of Mirbel, and these often sadly disfigured, copied without reflection.

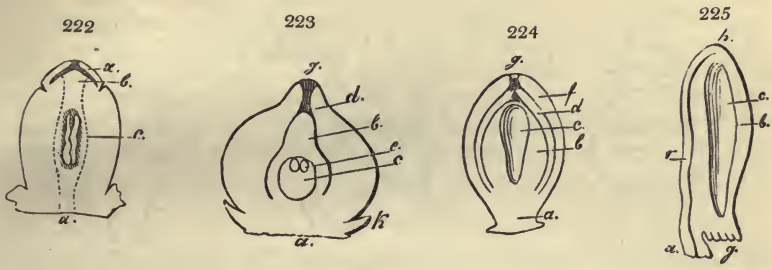
Using the observations of these men, I have made a large series of investigations upon the development of the unimpregnated seed-bud in plants of the most different families; and I have succeeded in verifying the laws which had been laid down, modifying them in some subordinate matters, and discovering a great body of facts, which are related in my two treatises, "Einige Blicke auf die Entwicklungsgeschichte, &c.," Wiegmann's Archiv., 1837, i. 289, and "Ueber Bildung des Eichens, &c.," Act. A. C. L. C. N. C., vol. xix. P. I., p. 29. I have stated the main points in the paragraphs. For the history of the development of a reversed seed-bud with two integuments I refer to Plate IV., with its explanation. I will now add a few remarks of subordinate importance.

The above-mentioned varieties of the seed-bud which arises from its curvature are only the main types, and by no means embrace all possible diversities; nay, are only arbitrary distinctions, since between each of those named occur intermediate forms which are difficult to reduce. No definite laws, therefore, can be laid down for the occurrence of particular forms, any more than for the number of integuments. Usually the same form is constant in the same family, yet it does sometimes exhibit deviations; this, however, less in Dycotyledons than in Monocotyledons: amongst the last, the family of the *Araceæ* especially exhibits an endless variety of forms of seed-bud. In order to aid the comprehension of the various forms of seed-buds, and to lead to the examination in actual specimens, I here offer some examples arranged as systematically as is possible. The seed-buds are exhibited cut accurately in half by a successful longitudinal section: —

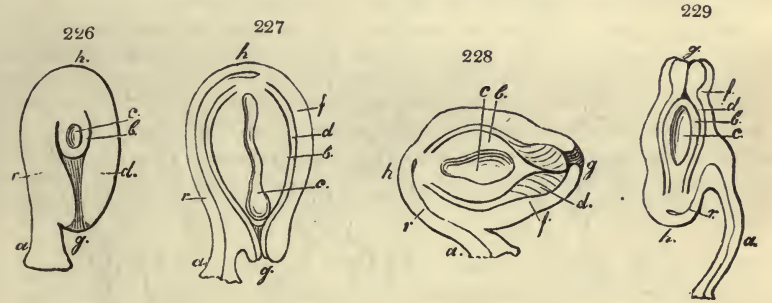
* Observations on the Organs and Mode of Fecundation in *Orchidaceæ* and *Asclepidaceæ*. London, 1831.

† Wiegmann's Archiv, 1835, vol. ii. p. 229.

1. Seed-buds not curved, as naked nuclei (fig. 222. *b*), or with one (fig. 223.) or with two integuments (fig. 224).




2. Reversed seed-buds, as naked nuclei (fig. 225.), or with one (fig. 226.) or with two integuments (fig. 227.).




3. Half-reversed seed-buds, with peltate mode of attachment (fig. 228.) and erect (fig. 229.).

[222] *Viscum album.* Longitudinal section through the female flower. *a*, Point of attachment (*hilum*) and chalaza; *b*, end of the floral axis as seed-bud, forming a straight naked nucleus; *c*, boundary of the pith in the pedicel, in which the embryo-sacs are also developed (two are shown in the figure); *x*, floral envelopes.

[223] *Taxus baccata.* Longitudinal section through the seed-bud. *a*, Hilum and chalaza; *b*, nucleus; *c*, embryo-sac; *d*, simple integument; *e*, large cells of the endosperm (*corpuscula* Robt. Brown); *g*, micropyle; and *k*, rudiments of the arillus.

[224] *Polygonum divaricatum.* Seed-bud in longitudinal section. *a*, Hilum and chalaza; *b*, nucleus; *c*, embryo-sac; *d*, inner, and *f*, outer integument; *g*, micropyle.

[225] *Hippuris vulgaris.* Seed-bud in longitudinal section. *a*, Hilum; *b*, naked nucleus; *c*, embryo-sac; *g*, nuclear papilla; *h*, chalaza; *r*, raphe.

[226] *Adoxa Moschatellina.* Seed-bud in longitudinal section. *a*, Hilum; *b*, nucleus; *c*, embryo-sac; *d*, simple integument; *g*, micropyle; *h*, chalaza; *r*, raphe.

[227] *Cucurbita Pepo.* Seed-bud in longitudinal section, some time after impregnation. *a*, Hilum; *b*, nucleus; *c*, embryo-sac; *d*, inner, and *f*, outer integument; *g*, micropyle; *h*, chalaza; *r*, raphe.

[228] *Lemna trisulca.* Seed-bud in longitudinal section. *a*, Hilum; *b*, nucleus; *c*, embryo-sac; *d*, inner, and *f*, outer integuments; *g*, micropyle; *h*, chalaza; *r*, raphe.

[229] *Meconostigma pinnatifidum.* Seed-bud in longitudinal section. *a*, Spermophore, funiculus, and hilum; *b*, nucleus; *c*, embryo-sac; *d*, inner, and *f*, outer integuments; *g*, micropyle: *h*, chalaza; *r*, raphe.

4. Curved seed-bud, as naked nucleus (fig. 230.), with one (fig. 231.) or with two integuments (fig. 232.).

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5. Semi-curved seed-bud, with one (fig. 233.) or with two integuments (fig. 234.).

6. Arched seed-bud, with two integuments (fig. 235.).

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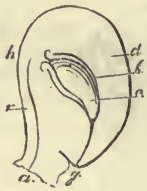


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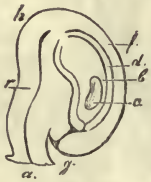


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7. Reversed seed-bud, with two integuments and an arillus (fig. 236.).

8. Doubly-curved seed-bud, with two integuments (fig. 237.).

9. Wholly abnormal, spirally-curved seed-bud, with two integuments (fig. 238.).

[230] *Galium Aparine.* Seed-bud in longitudinal section. *a*, Hilum and chalaza; *b*, naked nucleus; *c*, embryo-sac; *g*, papilla of the nucleus.

[231] *Datura Stramonium.* *a*, *h*, Hilum and chalaza; *b*, nucleus (as a nuclear membrane); *c*, embryo-sac; *d*, simple integument; *g*, micropyle.

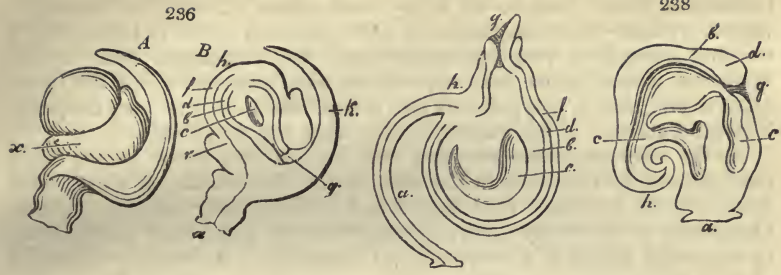
[232] *Spergula pentandra.* Seed-bud in longitudinal section. *a*, *h*, Hilum and chalaza; *b*, nucleus; *c*, embryo-sac; *d*, inner, and *f*, outer integument; *g*, micropyle.

[233] *Salvia officinalis.* Seed-bud in longitudinal section. *a*, Hilum; *b*, nucleus; *c*, embryo-sac; *d*, simple integument; *g*, micropyle; *h*, chalaza; *r*, raphe.

[234] *Colutea arborescens.* Seed-bud in longitudinal section. *a*, Hilum; *b*, nucleus; *c*, embryo-sac; *d*, inner, and *f*, outer integument; *g*, micropyle; *h*, chalaza; *r*, raphe.

[235] *Galphimia mollis.* Seed-bud in longitudinal section *a*, Funiculus and hilum; *h*, chalaza; *b*, nucleus; *c*, embryo-sac; *d*, inner, and *f*, outer integument; *g*, micropyle.

236 237 238




In the formation of the integuments, the conditions and relations of the individual parts particularly deserve a closer investigation.

In the first place, I must remark that the term nucleus, as used in contradistinction to the integuments, designates only that portion of the original little conical body, which, in the beginning above the integuments, becomes covered up by these, and to which the micropyle canal leads. The relative size and the form of this nucleus are very various; it usually forms a small ovate body, being thicker above the base, and then gradually narrowed towards its summit (fig. 239.); but it is also frequently a long cylinder (in many *Scrophulariacæ*, as, for example, *Pedicularis* (fig. 240.); frequently, it is a mere blunt cone (as, in *Podostemon*), or a hemisphere (as in *Convolvulus*, fig. 241.), or even little more than a mere point to which the micropyle canal leads, whereby alone such a seed-bud is distinguished from a naked nucleus (for example, in *Scabiosa*, fig. 242.).

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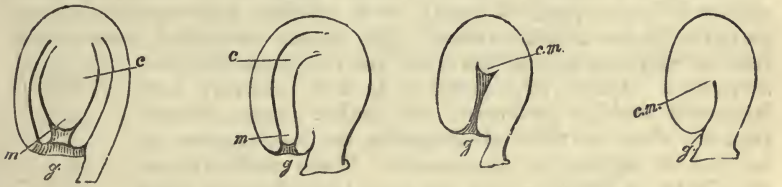


[236] *Hellenia cœrulea.* *A*, Seed-bud before impregnation: *x*, thickened border of the exostome. *B*, The same in longitudinal section: *a*, funiculus and hilum; *b*, nucleus; *c*, embryo-sac; *d*, inner, and *f*, outer integument; *g*, micropyle; *h*, chalaza; *r*, raphe; *k*, arillus.

[237] *Scleranthus perennis.* Seed-bud in longitudinal section. *a*, Funiculus and hilum; *b*, nucleus; *c*, embryo-sac; *d*, inner, and *f*, outer integument; *g*, micropyle; *h*, chalaza.

[238] *Lathræa squamaria.* Seed-bud in longitudinal section. *a*, Hilum; *b*, nucleus (as a nuclear membrane); *c*, embryo-sac, with its appendices; *d*, simple integument; *g*, micropyle; *h*, chalaza.

[239] *Lilium spec.* Seed-bud in longitudinal section. *c*, Nucleus; *m*, nuclear papilla; *g*, micropyle.

[240] *Pedicularis palustris.* Seed-bud in longitudinal section. *c*, Nucleus; *m*, nuclear papilla; *g*, micropyle.

[241] *Calystegia sepium.* Seed-bud in longitudinal section. *c*, *m*, Nucleus and nuclear papilla; *g*, micropyle.

[242] *Scabiosa atropurpurea.* Seed-bud in longitudinal section. *c*, *m*, Nucleus and nuclear papilla; *g*, micropyle.

No law can at present be laid down concerning the number of integuments, except that, so far as my observation extends, all Monocotyledons, without exception, possess two integuments, whilst in Dicotyledons we find sometimes two, sometimes one, and sometimes none at all. Speaking generally, we may say that in monopetalous plants the formation of one, and in polypetalous two integuments, are the more frequent. The total absence of integuments is the least frequent condition.

In the *Ranunculaceæ* one and two integuments occur in the same family; and, as I believe, in the same genus *Delphinium*, of which most species have two, but *D. tricorne* and *chilense* only one integument. Otherwise, so far as my knowledge extends, the number of integuments in the same family is a very constant character. A certain recognition of the very earliest conditions of the seed-bud is a matter of great difficulty in some plants, easy as it is in others; and the actual size of the parts to be investigated is by no means the cause of this. One of the smallest seed-buds and germens is, for example, presented by *Urtica dioica*, and yet this is one of the cases in which it can be traced; the isolation of a germen, and a slight pressure with a glass plate, suffice to make all clear. The difficulty is much more frequently caused by a very dense (preventing transparency) or very loose (interfering with certainty of the section) structure; by the form of the seed-bud (as in the *Asclepiadaceæ*) rendering the section of the seed-bud in symmetrical halves difficult; by the unsymmetrical arrangement, which renders the precise section into two halves, an impossibility (for instance, in *Veronica serpyllifolia*); by the nature of the contents of the cellular tissue destroying the transparency, and especially by the presence of much hairy structure from which the air can scarcely be disengaged, which makes observation impossible, and, even when the air is driven out, confuses the appearances by the irregular superposition. We often hear the following reasoning: "Since a matter could not be observed in such and such larger parts of plants, it is unlikely that any one has observed it in much smaller ones." My certain conclusion from this is, that he who thus argues has made but very superficial observations. Taught by experience, I, on the contrary, now frequently seek in preference the smaller plants, because they are often the most advantageous for investigation on account of needing no preparation. Water plants are especially to be recommended for most investigations, since their usually watery and transparent parenchyma greatly favours observation. These are unfortunately too little cultivated in our botanical gardens.

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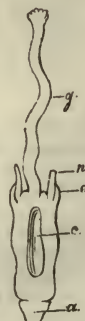


The common form of the papilla of the nucleus is that of a roundish hemispherical body (fig. 239. *m*); sometimes it is drawn out cylindrically, and then somewhat enlarged again at its extremity, as, for example, in the naked nucleus of *Loranthus*, where the point of the nucleus resembles a style in form (fig. 243. *g*).

Another point worthy of attention is the formation of the micropyle: this is commonly only a simple canal, the length of which is dependent merely upon the thickness of the integuments; sometimes, however, it is a large opening, from which the inner parts

[243] *Loranthus Deppeanus.* Part of the flower in longitudinal section. *a*, Pedicel; *c*, embryo-sac; *o*, *n*, floral envelopes and stamens, cut off; *g*, nuclear papilla, elongated so as to resemble a style.

project out more or less. This is often most striking in the external integument, which frequently leaves fully the half of the seed-bud uncovered, as in *Zea*, *Coix*, *Panicum* (fig. 244.). According to Brown, a similar condition occurs in the species of *Banksia* and some of those of *Dryandra;* however, from investigations made upon fresh flowering examples of *Banksia insularis* and *media*, I believe that I have a right to assert distinctly the contrary. On the other hand, I have examined an undetermined *Banksia* from the Berlin botanical gardens, in which it was certainly as Robert Brown states; but the seed-buds were suspended and half-reversed, whilst, with the two species of *Banksia* just mentioned, the seed-buds were erect and quite reversed. A remarkable form occurs in some *Abietineæ;* for instance, in *Abies* (fig. 245. *g.*) and

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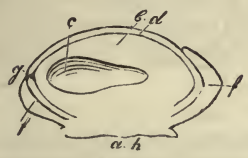


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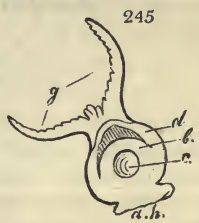


*Larix*, in which the micropyle is extended into two lobes, papillose, and secretes a fluid; and thus, from its similarity to a stigma, has been the greatest prop of the opinion that the integument is a germen. It is very common for the inner integument to project beyond the outer one, or at least to have its free border uncovered and lying in one plane with the outer integument. Where this occurs, it is common also to find the part of the inner integument forming the endostome swollen, so as to appear somewhat constricted by the rest. In *Araceæ*, *Liliaceæ* (fig. 246.), &c., this is very frequent. Occasionally, but less frequently, the exostome is swollen in a similar way: this occurs, however, in many *Euphorbiaceæ* (fig. 247.), (the so-called *caruncula* of the seed), as Mirbel has shown.

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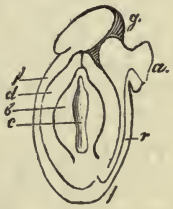


[244] *Panicum miliaceum.* Seed-bud in longitudinal section. *a*, *h*, Hilum and chalaza; *b*, nucleus; *c*, embryo-sac; *d*, inner, and *f*, outer integument, the last leaving the great part of the first uncovered; *g*, micropyle.

[245] *Abies excelsa.* Longitudinal section through the seed-bud, with the upper part of the micropyle (*g*) uninjured. *a*, *h*, Hilum and chalaza; *b*, nucleus; *c*, embryo-sac; *d*, simple integument.

[246] *Trillium erectum.* Seed-bud in longitudinal section. *a*, Hilum; *b*, nucleus; *c*, embryo-sac; *d*, inner, and *f*, outer integument; *g*, micropyle, formed solely by the inner integument; *h*, chalaza.

[247] *Euphorbia pallida.* Seed-bud in longitudinal section. *a*, Hilum; *b*, nucleus;

One of the rarest phenomena is that in which the formation of the outer integument begins higher up upon the seed-bud than the inner, so that the upper half of the nucleus is covered with two integuments, and the lower part only by a very thick, *simple* one, as is the case in the *Tropæolaceæ* (fig. 248.). A similar result occurs in *Ricinus* (fig. 249.)

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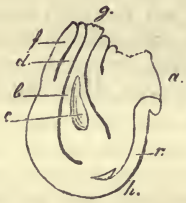


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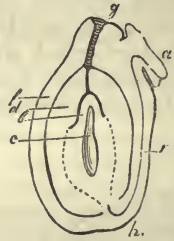


through the opposite process: here the outer integument commences much lower down than the inner one, and the upper part of the seed-bud exhibits two integuments, the under part only one, which is the *external* one.

In the presence of integuments, the relation of the chalaza to the rest of the seed-bud, which consists of nucleus and coats, varies exceedingly. The chalaza is usually confined to a small point at the base of the ovate nucleus; in the conical nucleus it occupies a greater portion, and in some plants (*Canna*), and even some families (*Compositæ*), it takes up half, or more than the half, of the entire seed-bud.

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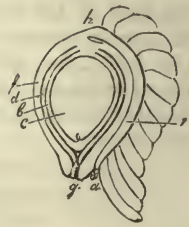


Lastly, it is to be mentioned, that on reversed seed-buds a peculiar cellular growth, termed a *crista*, is not unfrequently developed upon the raphe; it is sometimes narrow, resembling a cock's comb, as in the species of *Corydalis* (fig. 250.), sometimes thick and broad, so that the seed-bud itself appears but as a small appendage, as in *Aristolochia*. Sometimes, also, such a growth is formed like a collar around the entire seed-bud, or a part of its basis, as in *Hellenia*. Again, the funiculus has here and there sometimes peculiar hairy appendages, which often envelope the entire seed-bud, and almost always reach to the micropyle.

§ 162. The structure of the seed-bud is very simple; it consists of parenchyma and a distinct epithelium; this latter alone, as a mere fold, frequently forms the inner integument, probably in

*c*, embryo-sac; *d*, inner, and *f*, outer integument; *g*, micropyle, swollen; *h*, chalaza; *r*, raphe.

[248] *Chymocarpus pentaphyllus.* Seed-bud in longitudinal section, some time before impregnation. *a*, Hilum; *b*, nucleus; *c*, embryo-sac; *d*, inner, and *f*, outer integument; *g*, micropyle; *h*, chalaza; *r*, raphe.

[249] *Ricinus leucocarpus.* Seed-bud in longitudinal section. *a*, Hilum; *b*, nucleus; *c*, embryo-sac; *d*, inner, and *f*, outer integument; *g*, micropyle; *h*, chalaza; *r*, raphe.

[250] *Sanguinaria canadensis.* Seed-bud in longitudinal section, some time after impregnation. *a*, Hilum; *b*, nucleus; *c*, embryo-sac; *d*, inner, and *f*, outer integument; *g*, micropyle; *h*, chalaza; *r*, raphe, with a crest-like excrescence.

all (?) Monocotyledons. The simple integuments, the outer always and the inner sometimes, in *Thymelaceæ, Lauraceæ, Euphorbiaceæ,* and *Cistaceæ,* are composed of parenchyma, clothed on both surfaces with epithelium. Vessels and vascular bundles are *never* met with in nuclei or the integuments; usually, however, a vascular bundle traverses the funiculus and the raphe where they are present, but always terminates in the chalaza, frequently in a clavate group, or in a flat or concave expansion of spiral-fibrous cells. The funiculus is likewise clothed with epithelium, as an immediate continuation of the epithelium of the seed-bud.

The most important circumstance, however, is the change that takes place in the structure of the nucleus. Originally, this consists of a homogeneous, delicate, uniform parenchyma, but soon, and simultaneously with the first appearance of the integuments, one individual cell is excessively distended, displaces gradually more and more of the parenchyma around, which becomes dissolved and absorbed, and forms a cavity in the interior of the nucleus, clothed with a simple, structureless, membrane: this cell is the embryo-sac (*sacculus colliquamenti vel satius amnii* of Malpighi; the *quintine* of Mirbel, the *sac embryonnaire* of Brongniart.) Its form is very various, usually oval, often a slender filiform cell in the axis of the nucleus, the part towards the point of which is considerably swollen (as in *Amygdalus.*) Its contents are gum, sugar, or mucilage; very rarely it is gradually filled with cellular tissue before impregnation, as in the *Asclepiadaceæ.* In extremely rare cases (so far as is at present known, only in *Viscum*), two or three embryo-sacs are formed simultaneously.

The anatomical structure of the seed-bud is extremely simple, and I know of nothing important to be added to the above statements. Link says, "Where the funiculus enters the seed, a variously-shaped body often exists, which originates from the thickened and expanded funiculus, but clothed with an epidermis, of which the funiculus is destitute." Neither funiculus nor seed-buds or seeds, nor any part of them (with the exception of *Canna* and *Nelumbium*), have an epidermis with stomates. The funiculus is clothed by epithelium as well as the seed-bud (or the seed.) Link cites as an example, the *caruncula* in *Euphorbia* (which certainly, as I have already said, does not refer here), but in this very instance no epidermis, nay, even no epithelium, can be distinguished, since it is wholly composed of delicate, transparent, and somewhat elongated cells: on the other hand, the short thick funiculus has a most distinct epithelium in this very instance of *Euphorbia.*

The only essential anatomical point is the development of one cell of the nucleus into the embryo-sac.* This, so far as I can judge at present, exists in all *Phanerogamia* without exception; I venture to assert, that I have examined at least 500 plants of the most different families

* Link (Elem. Phil. Bot. ed. 2. vol. ii. p. 283.) says, "Malpighi's *sacculus colliquamenti,* which Robert Brown meant, Mirbel *not.*" Link has not read Mirbel properly: he expressly says, "*la quintine est la vésicule de l'amnios,* Malpighi," &c. Link further says, "This sac is filled with cellular tissue." This is untrue of at least one-tenth of the *Phanerogamia.*

(some 150), and have never failed, at least in earlier stages, to extract the embryo-sac uninjured, or at least in such large pieces that there can be no doubt of its existence. Meyen denies it in the *Liliaceæ;* I have already shown* how only most imperfect investigation is to blame for this. Link (El. Phil. Bot. ed. 2. ii. 283.) confounds every thing, because he evidently has made no *thorough* investigation himself, and therefore, copying Mirbel, Brown, and Brongniart, understood nothing of what they said. To enumerate all his errors and blunders here, would lead me too far; every one who knows the subject may readily compare Link and the authors named, and my explanations.

The observation is surest in *Lilium candidum* and most of the *Orchidaceæ*, since every cell of the nucleus has a distinct cytoblast here, therefore that cell also which expands to form the embryo-sac. By this means we are enabled always to recognise the tolerably perfect embryo-sac as a simple cell on account of its cytoblast. The demonstration of the embryo-sac is easiest in *Phormium tenax*, *Amygdaleæ*, *Nymphæaceæ*, and some *Cucurbitaceæ*, in which it may be exhibited free without much trouble. The form of the embryo-sac varies very much, partly depending on whether the cell which becomes converted into it lies nearest to the chalaza, the middle of the nucleus or the nuclear papilla. Very frequently it originally extends out into a cylindrical cell lying in the axis of the nucleus, which then becomes gradually widened from the summit (the part next the nuclear papilla) downward to the base; in some families this expansion is confined to the upper part, so that the lower portion appears like a filiform appendage to a large vesicle (*Amygdaleæ*, *Cucurbitaceæ*, *Nymphæaceæ*).

Great differences are manifested in the extent to which the nucleus is displaced by the embryo-sac. Sometimes the cellular tissue in the middle of the nucleus is connected into a closer and firmer ring around the embryo-sac, then usually also possessed of granular contents in this spot: thence the embryo-sac can only expand above and below this region, and thus acquire a lyrate form. In some families it displaces the nucleus very early, even to the extent of leaving only its epithelial layer, the nuclear membrane (*membrana nuclei*), which may then be readily overlooked (e. g. in the *Compositæ*); in others, this remnant of the nucleus becomes also displaced, and then, in the perfect seed-bud, the embryo-sac lies free in the cavity of the integuments (e. g. in the *Orchidaceæ*); in most of the *Leguminosæ* it does not stop here, but the internal integument becomes absorbed, sometimes from above downward, sometimes *vice versâ;* then a remnant of the cellular tissue of the nucleus sometimes remains upon the chalaza as a little conical body, so far as it surrounds the pointed lower extremity of the embryo-sac, e. g. in *Phaseolus.* In other families, too, a little papillary group of cellular tissue often occurs in the chalaza, which is persistent, and, since the embryo-sac displaces the cellular tissue in the circumference, projects as a little cone, clothed by the embryo-sac into its cavity, e. g. in *Hedychium.* The most remarkable phenomena occur in the *Scrophulariaceæ:* here the simple integument is very thick, the micropyle canal very long, and the nucleus a very slender longer or shorter cone, which is sometimes wholly displaced by the embryo-sac. As soon as this happens the apex of it extends out into the micropyle canal, and expands into a sac, displacing

* Wiegmann's Archiv, 1839, vol. i. p. 256.; Schleiden, Beiträge zur Botanik, vol. i. p. 40, et seq.

here a part of the integument (of the micropyle); in *Lathræa*, which plant has altogether a strangely aberrant form of seed-bud, there is formed, not merely here, but at the opposite extremity, a cæcal, sac-like appendix (fig. 238.).

Lastly, in the *Santalaceæ* it emerges from and lies quite free outside the micropyle as a sac of varying length.*

The formation of several embryo-sacs in *Viscum*, already mentioned, is at present peculiar to it. Meyen has the merit of first directing attention to it, and almost completely unfolding the particulars. In the beginning the cellular tissue of the pedicel of *Viscum* is perfectly homogeneous; by degrees an abundance of fluid is secreted between the cells lying in the axis; they separate from their union, and a kind of cavity is formed in which they lie loose. This I formerly†, before I had sufficient material for the history of development, erroneously stated to be the embryo-sac. Two or three of the loose cells in this cavity then expand into the form of tubes, which gradually displace the others (fig. 222.). All the rest, the gradual formation of cellular tissue, and the subsequent processes in the formation of the embryo, agree perfectly with those of other plants.‡ Only in a few cases does the embryo-sac, even at this period, become wholly filled with cellular tissue, but in a great many plants there begins at this time (as always happens later) a process of cell-formation, which constantly commences at the circumference of the cavity, and proceeds inwards; when a few layers of cellular tissue have been formed in this way upon the periphery, they represent what Mirbel has called the *quartine*, and from not having completely traced their development, has described as a fourth integument formed between the nuclear membrane and the embryo-sac. It is not a rare occurrence, and in the very family of *Cruciferæ* cited by Mirbel is easily traced in the way I have described it. There can be no question of integuments here. I will merely remark in passing that *every* embryo-sac subsequently becomes gradually filled with cellular tissue, which either becomes wholly displaced by the advance of the embryo or remains as endosperm (albumen); whether it appears somewhat earlier or later makes no difference. In the *Coniferæ* cellular tissue is likewise formed in the embryo-sac, which, however, becomes so arranged that from three to six larger cells immediately beneath the part turned toward the nuclear papilla, and clothed only by the embryo-sac on the outside, become especially strongly developed. The layer of cellular tissue which bounds these cells acquires an epithelial aspect, so that these cells appear like definitely bounded little sacs (Robert Brown's *corpuscula*.) I have

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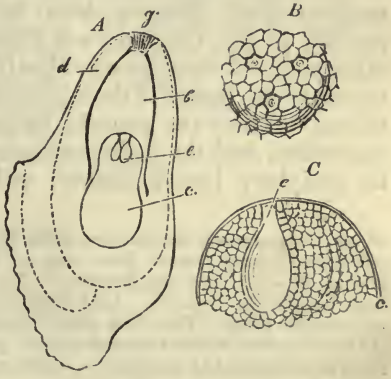


* Griffith on the Ovule of Santalum, Linn. Trans. vol. xviii.

† Wiegm. Archiv, 1839, vol. i. p. 212.; Schleiden's Beit. zur Botanik, vol. i. p. 21. pl. 2. fig. 15.

‡ Link (Wiegm. Archiv, 1841, vol. i. p. 393.), in opposing DeCaisne's very valua-

251 *Abies excelsa.* *A*, Seed-bud in longitudinal section; *b*, nucleus; *c*, embryo-sac;

traced the development of these completely in this way in our indigenous *Coniferæ*, particularly in *Pinus*, *Abies*, *Larix*, *Taxus*, *Thuja*, *Juniperus*, &c. In the young cells in the embryo-sac a circulation with reticular currents very often occurs (e. g. in *Ceratophyllum*, *Nymphæa*, *Nuphar*, *Pedicularis*, &c.). I have described the peculiar forms of this in *Ceratophyllum*, at length, in the Linnæa.

## III. *Of the Transformation and Development of the Parts of the Flowers into the Fruit.*

§ 163. Through manifold changes the individual parts of the fruit are developed out of the flower. The commencement of all these processes is, however, principally (in the natural conditions of plants, as wild, always?) connected with that circumstance which has hitherto been usually called the fecundation of plants. Here we have nothing to do with the *explanation* and *signification* of the phenomena therein occurring, but with the morphological development, which comprehends the four following sections: *A.* The change of place and development of the pollen to the embryonal globule. *B.* Development of the embryonal globule into the embryo. *C.* The perfecting of the germen and seed into fruit and seed. *D.* The phenomena exhibited in the other parts of the flower during these processes.

### *A.* THE CHANGE OF PLACE AND DEVELOPMENT OF THE POLLEN TO THE EMBRYONAL GLOBULE.

§ 164. As soon as the pollen is completely formed and the cells of the anthers have dehisced, the granules are brought in some mode or other, sooner or later, in the *Loranthaceæ* to the nuclear papilla, in the *Coniferæ* and *Cycadaceæ* to the micropyle, and in other plants to the stigma; or lastly, in the *Asclepiadaceæ* and *Apocynaceæ*, to the points of the stigmatic body which take the place of the stigma. There the granules lie for a variable time, then swell up somewhat, and the pollen-cell grows out gradually at one point of its periphery into a filiform cell (*tubus pollinis*, *tube pollinique*,

ble (but begun much too late) researches to Meyen's excellent essays, but without entering at all into Meyen's facts, says,—"If Meyen had continued his researches far enough, he would have seen his error." The very reverse, applied to DeCaisne's, would have been a just criticism. Link imagines that Meyen has not thought of the *pericarpium*, the berry. Has Link here thought of the juicy, berry-like seed of *Punica?* As if the pedicel in which an embryo has been formed may not become berry-like and juicy as the pedicel of *Anacardium*, which contains no embryo.

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*e*, corpuscula (R. Br.); *d*, simple integument; *g*, micropyle. *B*, Upper part of the embryo-sac seen from above: three orifices are perceived, formed of larger cells, characterised by the cytoblasts lying exactly externally. *C*, Upper part of the embryo-sac in longitudinal section. *c*, Embryo-sac; *e*, corpusculum (R. Br.); another, on the right side, shows through the cellular tissue, which fills the embryo-sac.

*boyeau*, pollen-tubes, *budelli pollinici*). In the three first-named families this penetrates immediately into the nuclear papilla; in the rest it follows the conducting cellular tissue, sometimes growing forth on its surface, sometimes penetrating through its loosened cells, till it reaches the cavity of the germen, and here penetrates through the micropyle, or immediately into the nuclear papilla of the seed-bud.

Whether and how the embryo originates from the pollen-tube is in the first place dependant on the question, whether and how the pollen-tube in each case reaches the micropyle and the papilla of the nucleus; and it is important for the establishment of the facts to separate the two questions completely from each other. The first question, how the pollen-cell deports itself on the stigma, I believe I may answer as in the paragraph, for *all* Phanerogamia, without exception; on this point, I think, the facts now lying before us can leave no doubt; it were rather to be wished that all our inductions in Botany were as well supported. For the illustration of this process may serve a preparation of *Helianthemum denticulatum* (fig. 252.), in which plant I have not unfrequently extracted the pollen-tube free, in unbroken continuity from the pollen-grain to the seed-bud. I refer also to Plate IV. figs. 1—3., with their explanation. However, it appears to me to be to the purpose to give a review of the observations on which my statements are founded. In the following plants of the following families I have traced the pollen-tube from the stigma into the micropyle; in those marked with an asterisk I have frequent, isolated the pollen-tube, in complete, unbroken continuity from the pollen-granule to the seed-bud.

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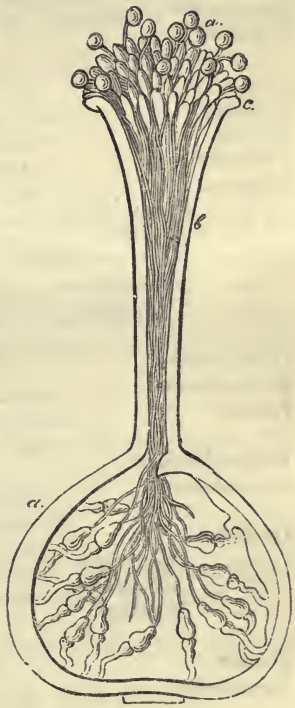


GYMNOSPERMÆ.

| *Families.* | *Species.* |
|---|---|
| Abietineæ.* | Larix europæa, Abies pectinata, alba, excelsa, Pinus sylvestris, uncinata. |
| Cupressineæ.* | Taxus baccata, Juniperus communis, sativa, virginiana, Thuja orientalis, Callitris quadrivalvis. |

[232] *Helianthemum denticulatum.* The pistil, in longitudinal section. *a*, Germen; *b*, style; *c*, stigma; *d*, pollen-granules, the tubes of which descend in the germen as far as the seed-buds.

MONOCOTYLEDONEÆ.

| *Families.* | *Species.* |
|---|---|
| Lemnaceæ. | Lemna gibba, trisulca. |
| Pistiaceæ. | Pistia commutata, obcordata. |
| Aroideæ. | Ari spec., Cryptocoryne spiralis, Sauromatum guttatum.* |
| Typhaceæ. | Sparganium natans. |
| Orontiaceæ. | Pothos reflexa, Orontium aquaticum.* |
| Najadeæ. | Zannichellia repens, Potamogeton lucens, heterophyllus, Caulinia fragilis, Aponogeton distachyon.* |
| Alismaceæ. | Alisma Plantago. |
| Junceæ. | Luzula pilosa. |
| Philhydreæ. | Philhydrum lanuginosum. |
| Liliaceæ. | |
| — Phormiaceæ. | Phormium tenax.* |
| — Aloineæ. | Gasteria subverrucosa. |
| — Hemerocallideæ. | Agapanthus umbellatus, Funkia cœrulea. |
| — Asphodeleæ. | Eucomis punctata. |
| — Tulipaceæ. | Tulipa sylvestris*, Breyniana*, Tupistra squalida. |
| Colchicaceæ. | Colchicum autumnale.* |
| Bromeliaceæ. | Tillandsia amœna. |
| Irideæ. | Sisyrinchium anceps, Gladiolus psittacinus.* |
| Hydrocharideæ. | Stratiotes aloides. |
| Scitamineæ. | Canna Sellowii, Maranta gibba, Hedychium Gardnerianum. |
| Orchideæ. | |
| — Ophrydeæ. | Orchis morio*, latifolia, palustris. |
| — Arethuseæ. | Epipactis palustris. |
| — Neottieæ. | Neottia picta, Goodyera discolor, Prescotia plantaginea. |
| Palmæ. | Chamædorea Schiedeana. |
| Gramineæ. | Zea mays, Phleum pratense, Bromus mollis, Elymus arenarius, Secale cereale. |
| Cyperaceæ. | Carex acuta.* |

DICOTYLEDONEÆ.

| | |
|---|---|
| Nymphæaceæ. | Nuphar luteum. |
| Ranunculaceæ. | Thalictrum petaloideum, Aconitum Napellus. |
| Papaveraceæ. | Papaver Rhœas, Argemone Hunnemanni, Chelidonium majus, Sanguinaria canadensis, Eschscholzia californica. |
| Cruciferæ. | Matthiola incana, Capsella bursa-pastoris. |
| Resedaceæ. | Reseda odorata. |
| Passifloreæ. | Passiflora princeps. |
| Cucurbitaceæ. | Pepo macrocarpus, Momordica Elaterium. |

DICOTYLEDONEÆ—(*continued*).

| *Families.* | *Species.* |
|---|---|
| Cacteæ. | Cereus grandiflorus. |
| Santalaceæ. | Thesium intermedium, linophyllum. |
| Ceratophylleæ. | Ceratophyllum demersum. |
| Podostemeæ. | Podostemon ceratophyllum. |
| Thymeleæ. | Daphne Mezereum, alpina. |
| Phytolacceæ. | Phytolacca decandra.* |
| Polygoneæ. | Polygonum orientale, divaricatum. |
| Nyctagineæ. | Mirabilis Jalapa, longiflora*, Oxybaphus chilensis. |
| Limnanthaceæ. | Limnanthes Douglasii. |
| Euphorbiaceæ. | Euphorbia pallida. |
| Cistineæ. | Helianthemum lasiocarpum*, denticulatum*, mutabile.* |
| Lineæ. | Linum pallescens. |
| Tropæolcæ. | Tropæolum majus. |
| Malvaceæ. | Hibiscus Trionum, Lavatera thuringiaca. |
| Sterculiaceæ. | Theobroma Cacao. |
| Rosaceæ. | Rubus cæsius. |
| Amygdaleæ. | Prunus Armeniaca, Padus. |
| Leguminosæ. | Cicer arietinum, Phaseolus vulgaris, Tetragonolobus purpureus, Baptisia exaltata, Lupini spec. |
| Illecebreæ. | Spergula pentandra. |
| Scleranthaceæ. | Scleranthus perennis. |
| Sileneæ. | Lychnis dioica, Saponaria officinalis. |
| Alsineæ. | Alsine media. |
| Callitrichaceæ. | Callitriche stagnalis. |
| Portulaceæ. | Calandrinia speciosa. |
| Staphyleaceæ. | Staphylea pinnata. |
| Onagreæ. | Œnothera Sellowii, viminea, crassipes*, Simsiana, rhizocarpa, Epilobium hirsutum. |
| Halorageæ. | Hippuris vulgaris, Myriophyllum spicatum. |
| Trapaceæ. | Trapa natans. |
| Loaseæ. | Loasa bryoniæfolia, Mentzelia hispida. |
| Plumbagineæ. | Armeria vulgaris. |
| Rubiaceæ. | Galium Aparine. |
| Umbelliferæ. | Peucedanum officinale. |
| Stylidieæ. | Stylidium adnatum. |
| Lentibulariæ. | Pinguicula vulgaris. |
| Violaceæ. | Viola tricolor. |
| Primulaceæ. | Hottonia palustris. |
| Ericeæ. | Monotropa Hypopitys. |
| Pedalineæ. | Martynia diandra. |
| Labiatæ. | Salvia bicolor. |
| Boragineæ. | Echium vulgare, Symphytum officinale. |
| Orobancheæ. | Lathræa Squamaria. |
| Scrophularineæ. | |
| — Salpiglossideæ. | Salpiglossis hybrida. |
| — Digitaleæ. | Chelone rosea. |

DICOTYLEDONEÆ—(*continued*).

| *Families.* | *Species.* |
|---|---|
| Scrophularineæ: | |
| — Rhinantheæ. | Pedicularis palustris, Melampyrum pratense. |
| — Veroniceæ. | Veronica hederæfolia, serpyllifolia. |
| Solaneæ. | Datura Tatula.* |
| Polemoniaceæ. | Phlox paniculata. |
| Cuscutaceæ. | Cuscuta europæa. |
| Gentianeæ. | Gentiana lutea. |
| Apocyneæ. | Vinca rosea, minor, Nerium Oleander. |
| Asclepiadeæ. | Asclepias pulchra, Cynanchum nigrum, Stapelia deflexa, Asterias. |
| Campanulaceæ. | Campanula Medium*, rapunculoïdes. |
| Compositæ. | Achillea Eupatorium, Hypochœris radicata, Carduus nutans.* |

To the preceding list I must subjoin the following observations: — *Pistia commutata* I examined in dried specimens; *Pistia obcordata, Cryptocoryne spiralis,* and *Podostemon ceratophyllum* in specimens which had been preserved in spirit. Otherwise the list is to be regarded merely as an enumeration of certain examples, since, during the last year or two I have not thought it worth the trouble to continue any longer the formerly rigidly kept list concerning this one fact, which is already put beyond a doubt by it; and I must have named a great number of additional families and species from memory, which I do not consider to the purpose. The majority of the foregoing observations were made in Berlin, and I made use of my uncle Horkel constantly as a *testis omni exceptione major*, and therefore most of the facts are to be regarded as certified by him also, as he has already openly stated.* From other quarters come the following confirmations. In the first place, Rob. Brown for the *Asclepiadaceæ* and *Orchidaceæ;* Wydler for the species of *Scrophularia,* Griffith for the *Santalaceæ.* Brongniart's observations also, of the pollen-tube hanging from the micropyles may now be added to these, although *he* had a different view of their origin; consequently the families of the *Cucurbitaceæ, Polygonaceæ, Euphorbiaceæ* and *Convolvulaceæ;* further, Amici for *Yucca gloriosa* and many other plants not specially named by him; lastly, Meyen must be named, although, in the whole of his somewhat confused exposition of fecundation and formation of embryos, he constantly speaks of the universality of the descent of the pollen-tube, but does not mention one single plant definitely in which he had actually observed it: on the other hand, he cites a large number of plants of the above-named families, as well as of some others, in which he had observed the pollen-tube to enter into the micropyle.

Easy as the observation is in some families, it is very difficult in others; not only the same circumstances occur here as in the tracing of the canal of the style from the stigma to the cavity of the germen, but it requires very much greater delicacy and skill in manipulation, to lay the conducting tissue bare in large pieces in such a manner that it may be conveniently separated under a simple microscope, and the pollen-tubes be extricated. While in some plants, *Orchidaceæ, Datura, Œno-*

* Monatsberichte der Berliner Academie der Wissenschaften, Aug. 1836.

*thera*, *Helianthemum*, (fig. 251.), I pledge myself to lay bare the tube from the stigma to the seed-bud in a few minutes, which plants I select annually for demonstration in my Lectures, in others I have often dissected a week, and even a fortnight, from early till late, before I once succeeded in perceiving, with full certainty, the whole course of the pollen-tube. Nay, sometimes my observations have remained quite imperfect in one year, and only been completed by resuming them in the following. I remark this here, because I find that many imagine the matter to be very easy, and when they have not succeeded in the first attempt, think at once their negative observation has sufficient value to set aside the assertion of others, while it only bears testimony to their want of skill or impatience, and this indeed most decidedly.* The best method of proceeding is to cut from the axis of the entire pistil, with a broad, sharp knife (I always use a razor), a lamella, not too delicate, so that the section may contain part of the stigma and the conducting tissue, as perfect as possible, down to the seed-bud. This section must then be brought under the simple microscope, and the whole of the pollen-tubes present separated with the needle from the cellular tissue on which they lie, beginning at the stigma and proceeding to the seed-buds; then the funiculus of these is to be cut away from the spermophore, taking care not to cut through the pollen-tubes at the same time, and the attempt made to separate the single tubes from each other until you are guided by one of these to the micropyle. One must frequently be content to perform the operation piecemeal, by examining, one after another, as long pieces as possible of the conducting tissue, from the stigma to the seed-buds, and thus to make sure of the complete descent of the pollen-tube. The search for and tracing of the tubes is most facilitated, especially in the *Dichogameæ*, *Monöcistæ*, and *Diöcistæ*, by applying the pollen of recently-burst anthers to a perfectly developed stigma, and then examining at different periods. The time required to complete the process of growth varies very much: in the style of *Cereus grandiflorus*, nine inches long, the end of the pollen-tube reaches the seed-bud in a few hours; in that of *Colchicum autumnale*, of thirteen inches long, in about twelve hours; in others it is often weeks before it has traversed the very short distance. Besides, the pollen-granules, which are also often carried to the stigma at different times, do not all grow down simultaneously. Finally, the persistence of the upper end, which still sticks or did stick in the pollen-granule, varies much; while in some plants the pollen-tube remains perceptible in its whole length for weeks, in others it dies away above almost as fast as it grows below. In plants of which the stigmatic fluid hardens into a kind of membrane, the portion of the tube between this membrane and the pollen-granule often remains visible for a long time, while the portion from the membrane to

* This difficulty in the investigation, which only occurs in certain cases, is by no means the reason why in this, the most important of all studies, from 1823, when the question was raised by Amici's discoveries, to 1842, only five, say five, men can be named who have contributed to its progress: but the usual indifference of most botanists to all deeper and really scientific investigations. How essentially the answering of the whole question is thereby modified, whether the stigma is clothed by a dense, structureless membrane, is evident. Brongniart had asserted the existence of such a membrane in *Nymphæa*, *Hibiscus*, and *Mirabilis*, in 1827: in 1837 Link said, "According to Brongniart, it is so." Therefore, during ten years, he had not thought it worth the trouble once to look into these plants, which are everywhere to be found, to confirm or refute Brongniart's opinion. Is anything like this really heard of in any other branch of natural science?

the growing extremity soon decays, e. g. in *Nymphæa, Mirabilis,* &c. The differences stated render it wholly impossible to give safe indications *à priori* for all plants. Patience is necessary, not to be frightened by frequent abortive attempts, till we have learned from the plant itself its peculiarity: whoever has not this patience will not do for an investigator of nature.

Many have referred to another difficulty in the observation of the pollen-tube, which, from my own investigations, cannot at all be considered as such, namely, the possible confusion of the cells with the conducting tissue for the pollen-tubes. I have never yet met with a plant in which such a mistake was possible; the cells of the conducting tissue are always twice or three times as thick as the pollen-tubes of the same plant: in no plant are those cells longer than very much elongated parenchyma-cells, i. e. about one-tenth of a line, and therefore every pollen-tube may be recognised at once by the continuity of the cavity through longer tracts. The lament over the possibility of that error has arisen solely from very bad methods of investigation. He who takes an impregnated plant, and hastily examines a longitudinal section from the style, may perhaps doubt whether he has an elongated cell or a pollen-tube before him; but — and this is the only proper way — he who first traces the development of the pistil in all its parts up to the time of flowering, and then, well acquainted with the existing condition, examines an impregnated pistil, perceives in a moment what new elements have entered into the style, and cannot imagine the possibility of a confusion of the pollen-tubes with the conducting tissue. Lastly, I must confirm the opinion which Horkel has expressed, that Rob. Brown's "mucous tubes" are nothing else but the pollen-tubes, the connection of which with the pollen-grain is already destroyed. Within a certain time after impregnation all the pollen-tubes of the *Orchidaceæ* become mucous tubes, because they begin to decay from without inward.

Meyen says that he has frequently seen branched pollen-tubes: I have never met with them, but I consider them very possible. Only in the neighbourhood of the seed-bud, or quite inside the micropyle, I have sometimes seen a very short blind lateral branch given off by a pollen-tube, and, in general, the otherwise pretty smooth and cylindrical tubes here very frequently exhibit irregular curves and varicosities. In the earliest stage of formation of the tube, the contents of the pollen-tube usually exhibit an active circulation, which, however, soon ceases; by degrees the contents becomes concentrated down into the apex of the tube, partly unaltered, partly chemically changed into other matters, often dissolved into a perfectly transparent watery fluid.

It is well-known that the pollen-granules swell up and burst through endosmose in water, and the coagulating contents are emitted in an intestine-like form, but this has nothing to do with the formation of the tube on the stigma; on the other hand, true tubes may be obtained from almost every kind of pollen, for clearer observation than is generally possible on those taken from the stigma, by laying them in the sweet juice which is secreted by some plants, e. g. in the nectary of the Crown-imperial, the abundant nectar of *Hoya carnosa,* &c., or sometimes even merely in sufficiently concentrated solution of sugar or diluted honey. In these it usually is easy to see the circulation of the contents of the pollen-cell in the formation of the tube, first observed by Amici. Without human interference also, pollen-grains, which come accidentally in contact with nectar, readily send out tubes, and we often find at the

base of the flower a whole mass of confervoid web, which consists of entangled pollen-tubes emitted in this manner. Nay, in the anthers of the *Aristolochiacæ*, which usually secrete some sweet juice, the pollen not unfrequently emits tubes, which then, as I believe to have seen, come by chance over the border of the anther on to the stigma, and so descend into the cavity of the germen without waiting for the insects which here so abundantly assist.

### *History and Criticism.*

In many plants the pollen-tubes are so striking, even by their mass, that, although every possible opinion but the true one was entertained as to the behaviour of the pollen to the stigma, they could not have been wholly overlooked, if it had only happened to the few microscopic observers of the eighteenth century to have examined the localities in which they occur. Horkel (*op. cit.*) has collected the earliest traces of observation of them: Amici* made the discovery that a tube is emitted by the pollen-granule and penetrates between the papillæ of the stigma; and was also the first who traced the pollen-tube from the stigma to the micropyle, probably in *Yucca gloriosa.*† In the interval between these observations, however, Brongniart‡ had made known his far more comprehensive researches, in which he observed the pollen-tube everywhere on the stigma, and in many plants as torn extremities hanging out from the micropyle. These two torn ends were then united by Rob. Brown§ (1831, 1832, 1833) in applying Amici's discovery, with his well-known profundity and accuracy, to two of the most widely distinct families, the *Asclepiadaceæ* and *Orchidaceæ*, and in both he placed the growth of the pollen-tube into the seed-bud beyond doubt. I myself have extended Rob. Brown's observations to a great number of families, and these observations, confirmed by Horkel, were made known by him in the Monthly Report of the Berlin Academy of Sciences, in August 1836, and by me in Wiegmann's Archives for 1837 (vol. i. p. 312. *et seq.*). Horkel's paper appears to have remained wholly unnoticed, and thence many may have thought that they might quietly set aside my observations, to put their crude observations, or often mere opinions, in their place. Nevertheless, I might leave mine to themselves as incontestible, under the ægis of observers like Amici, Rob. Brown, and Horkel. Finally, Wydler‖ of Bern observed the descent of the pollen-tube and its entry into the seed-bud in several species of *Scrophularia;* and Meyen likewise confirmed the correctness of the existing observations, without specially naming the plants in which he had completely traced the pollen-tube, but giving abundance of matter in the shape of observation of the entry of undoubted pollen-tubes into the micropyle. Thus the fact, that in all Phanerogamia the pollen-tubes descend to the seed-bud was admitted as a law, till recently Hartig¶ appears to have intended to upset the whole matter. In the first place, it cannot but awaken a prejudice against his book, that instead of relating unbiassed and accurately-observed facts, he at once spins out a new so-

* Mem. di Soc. Ital. v. xix. pp. 253—257. (1823).

† Ann des Sc. Nat. v. xxi. p. 331. (1830).

‡ Mém. sur la Génération et le Développement de l'Embryon, &c. Paris, 1827.

§ Observations on the Organs and Mode of Fecundation in Orchideæ and Asclepiadeæ. London, 1833.

‖ Bibliothèque Univers. de Genève, Oct. 1838.

¶ Neue Theorie der Befruchtung der Pflanzen, &c. Brunswick, 1842.

styled theory, and, moreover, gives an extensive new terminology. Hartig certainly speaks of many new discoveries, but if one looks into the matter, not one single fact is found which was not better understood before. The complete uselessness of this book to the advancement of our science follows from two circumstances: in the first place, the author's total ignorance of the literature of the subject, of what has been established by those who have worked in the science before him; in the second place, Hartig evidently has not the necessary skill in manipulation, nor a correct method. Therefore his whole work in fact only says, "I have not succeeded in tracing the pollen-tubes in the generality of plants;" on which it is to be remarked, that he sought partly in the wrong places, and partly (as in the Dichogamous flowers) at the wrong time; hereupon he at once assumed a new mode of fecundation, where he saw the pollen-granules lie and dry up, or emit imperfect tubes. Hartig has himself such clear and correct reasoning in his Introduction, that he may be readily confuted by it. He states the question thus: Can the rudiment of the embryo lie sometimes in the pollen-tube, and in others in the germen, in the seed-bud? and with perfect right answers in the negative; since there exist no grounds for assuming such a planless uncertainty in nature. Then Hartig proceeds: If now an undoubted case exists, in which the embryo cannot originate from the pollen-tube, its origin from that is consequently to be universally denied. This is quite right too, only, from the greater value and easier proof of positive assertions, it would be better to state the matter the reverse way. If, namely, the origin of the embryo from the pollen-tube has been observed undoubtedly in but one case, the matter is decided, and all apparently opposing facts fall into the class of imperfect observations. Such cases actually do exist, even if I disregard my own observations, quite clear and admitting of no other signification; Wydler has furnished in *Scrophularia,* and Meyen in *Fritillaria imperialis,* the most complete testimony, and Meyen's observation is especially the more decisive, that he, starting from a pre-conceived notion, neither expected such a result from the investigation, nor could admit it, and therefore took every pains to explain away those facts which he was much too candid to suppress. Thus is the question decided on the ground which Hartig himself has given. He thinks, however, he can give the decision quite the other way, in ignorance of those facts and referring to his observations of *Companula,* as he himself owns, the *sole sure* prop of his different theory. This pillar, however, is very weak; the peculiar behaviour of the collecting hairs, observed long before his researches, has nothing at all to do with fecundation, or, at most, only so far that in the retraction of the hairs the greater part of the pollen becomes stripped off them, and thus exposed loose to the wind and insects, which transport it to the stigma.* The fecundation of the *Campanulaceæ* takes place in quite a different way. By industrious and patient search I have always found the pollen-tubes on the stigma and at the micropyle in the *Campanulaceæ;* in *C. Medium* and *rapunculoides* I have traced them the whole way; in the former it is not even difficult to demonstrate the whole tube in unbroken continuity. I doubt not too, that Hartig, who is earnest and zealous in science, will before long become convinced of the untenable nature of his imaginary theory. I consider it quite superfluous to enter further into Hartig's views, since the whole relates merely to imperfect

* Wilson (Mohl und Schlechtendahl's Bot. Zeitg. vol. i. pp. 382. and 870.) has also shipwrecked his skill in observation on the collecting hairs of the *Campanulaceæ.*

perception of facts long since better understood. Hartig has attempted a rather unfortunate defence of his "theory."* I think that I have wholly settled the matter in my answer.†

§ 165. The pollen-tube, which has arrived in the seed-bud in the manner above stated, either at once meets the embryo-sac, or penetrates through the intercellular passages of the cellular tissue of the nuclear papilla, which becomes somewhat more lax about this time through a secretion, till it reaches the embryo-sac.

The next phenomenon is the appearance of the end of the pollen-tube inside the embryo-sac as a cylindrical or ovate utricle of variable length, which has a round closed extremity toward the cavity, and at the apex of the embryo-sac runs up open into the pollen-tube; the extremity soon swells up, either in such a manner that the utricle produced by it (embryonal vesicle, *keimbläschen*) consists of the whole of that part of the tube within the embryo-sac, or so that between this utricle and the apex of the embryo-sac there remains a cylindrical piece, of variable length, the embryophore (*keimträger, embryoträger, filamentum suspensorium, filament suspenseur,* Mirbel). The cellular tissue is developed in the interior of the pollen-tube, cytoblasts originating and cells being developed from them. Since new cells originate inside these cells, and so forth, the embryonal vesicle, by gradual increase of size and reabsorption of the parent-cells, at last becomes a little globular or ovate cellular corpuscule. The pollen-tube is usually constricted and closed outside the embryo-sac at the same time, and becomes absorbed; frequently also, especially where an embryophore or suspensor exists, the embryonal vesicle itself becomes constricted and detached, and then lies perfectly free in the apex of the embryo-sac.

The investigation of the processes described in these paragraphs is without doubt, next to the origin of new cells in crowded parenchyma, the most difficult task in Botany. Since I made those facts known, a great deal has indeed been said on the matter; but of the many hundreds of botanists, only a few have made careful investigations of the kind. The following are the plants in which I have, up to this time, completely examined the formation of the embryonal vesicle from the end of the pollen-tube, in such a manner that I have extracted the already perfectly distinct embryonal vesicle, perceptible in the embryo-sac, in completely uninjured continuity with pollen-tube, still existing at least outside the nucleus, quite free, — and afterwards traced the origin of the embryonal globule, by the formation of cells *in the* embryonal vesicle: —

*Phormium tenax, Eucomis punctata, Sisyrinchium anceps, Stratiotes aloides, Canna Sellowii, Maranta gibba, Orchis Morio* (Plate V. figs. 10, 11.), *latifolia* (Plate VI. figs. 1, 2.), *palustris, Zea Mays, Nuphar luteum, Momordica Elaterium* (Plate VI. figs. 9—11.), *Daphne Mezereum, Phytolacca decandra, Polygonum orientale, Mirabilis Jalapa, longiflora,*

* Hartig, Beit. zur Entwicklungsgeschichte der Pflanzen. Berlin, 1843.

† Die neuern Einwürfe gegen meine Lehre von der Befruchtung, &c. Leipsic, 1844.

*Limnanthes Douglasii*, *Linum pallescens*, *Tropæolum majus*, *Cicer arietinum*, *Phaseolus vulgaris*, *Œnothera viminea*, *crassipes*, *rhizocarpa* (Plate VI. figs. 7, 8.), *Martynia diandra* (Plate VI. figs. 5, 6.), *Salvia bicolor* (Plate VI. figs. 3, 4.), *Lathræa Squamaria*, *Veronica hederæfolia*, *serpyllifolia*, *Pedicularis palustris*, *Cynanchum nigrum*, *Campanula Medium*, *Tetragonia expansa*, *Epilobium hirsutum* (Plate V. figs. 7, 8.).

In many of these plants I have laboured in vain for many years; in some I have oftener succeeded in observing the whole process without the possibility of deception: I have never yet found any plants in which the observation is so easy, that I could say that I could at any time prepare the necessary dissection with certainty; I have found it easiest in *Œnothera*, *Veronica*, *Pedicularis*, and the *Orchidaceæ*. If *Santalum album* were at our command, we should probably have a plant in which we could at any time demonstrate the process with certainty. Perfect confirmation of the main point, namely, the conversion of the end of the pollen-tube into the embryo through internal processes of vegetation, have been furnished by Wydler* in some species of *Scrophularia*, by Meyen† in *Fritillaria imperialis* and *Tulipa*, and by Gelesnoff‡ in *Amygdalus persica*, *Iberis amara* and *umbellata*. The observation of Meyen is the better evidence that it came certainly quite unsought for; since it is alone quite sufficient to refute his very artificial, and, I will openly confess, to me thoroughly incomprehensible, explanation of his other less perfect observations. The figures 37—43. Plate XIII., from *Alsine media*, of Meyen, also agree tolerably perfectly with my observations, only I do not rightly know what to make of figures 38 to 41. I must confess that it has hitherto always appeared to me impossible to prepare it free in so early a condition in *Alsine media*, and these observations do not at all agree with Meyen's explanation; moreover, figs. 21—23. from *Draba verna*, fig. 34. from *Orchis Morio*, fig. 44. from *Helianthemum canariense*, fig. 48, 49. from the same plant, only the order is evidently different; fig. 49 is an earlier condition, fig. 48 the commencement of the constriction of the pollen-tube; lastly, also, (Polyembryonie, &c., Plate I.), from *Viscum album*, on which I will merely notice that fig. 8. is evidently later impregnated, and an earlier stage of formation than fig. 7., which follows from the fact that the membrane of the embryo-sac is not yet completely absorbed, and therefore still surrounds the contained cells with a smooth outline. All the rest of Meyen's figures exhibit only later conditions, after the separation of the pollen-tube outside the embryo-sac, often even after the separation of the germinal vesicle inside it. Lastly, Griffith§ has instituted researches on this process in *Santalum album*, and indeed earlier, before my observations were made known; unfortunately, he evidently had not a good microscope at his command, and he is candid enough not to describe, or draw as definitely seen, anything which remained indistinct to him. *Santalum album* is certainly a most advantageous plant for these researches. The allied species of *Thesium* present great difficulty. On the other hand, Martius‖, in the year 1844, published the following passage of a letter from Griffith: "A year ago I sent an extended essay

* Loc. cit.

† Physiologie, vol. iii.; and Ueber den Befruchtungsact und die Polyembrionie, &c. Berlin, 1840.

‡ Botan. Zeitung, vol. i. p. 841.

§ On the Ovulum of Santalum album, Trans. Roy. Soc. vol. xviii.

‖ Munich gel. Anzeig. No. cxliii. p. 107.

on fecundation to the Linnæan Society, in which Schleiden's view of the origin of the embryo from the pollen-tube is confirmed. The observations in *Santalum* are the most sure. In *Loranthus* the pollen-tubes undoubtedly traverse the whole embryo-sac."

After this exposition, I must now regard the formation of the embryo from the pollen-tube as completely established, and observations disagreeing with this can hereafter only be of value if they at once completely explain the cause how an error, of course not absolutely impossible, could conceivably have arisen in the minds of so various, truth-searching, and, with respect to Meyen in particular, certainly unprejudiced observers. But if science is actually to advance, all boldly-expressed fancies, based on a few imperfect observations, in total ignorance of what has been done before, must be wholly excluded. This especially applies to the trifling, though very pretentiously delivered, new researches of Amici.* It is very sad, that in a whole association of naturalists there was not a single one who had the most distant idea of the imperfection of this essay, or, at all events, expressed it. See my observations on that Essay in the "Flora."†

With regard to particular points in the processes described, the following questions may yet be raised. In the first place, the mutual behaviour of the embryo-sac and the pollen-tube is by no means perfectly cleared up yet by observation. It remains undecided, in certain cases, whether the membrane of the embryo-sac, which in this way becomes pushed inward and forms an investment over the apex of the pollen-tube, does not subsequently perhaps become dissolved and absorbed, so that the pollen-tube actually penetrates directly into the cavity of the embryo-sac, which is certainly very probable in those plants in which the pollen-tube goes down a disproportionately long way into the embryo-sac, as in many species of *Veronica*, in the *Santalaceæ*, in *Martynia diandra*, where it descends almost to the chalaza; in some, e. g. in *Phormium tenax*, a distinct investment of the pollen-tube clearly remains for a long time. This much is certain, that in all cases where I was certain that the object was still in its natural position, especially where I succeeded in laying bare the apex of the embryo-sac and pollen-tube in the section, without removing them from their proper places in the seed-bud, I saw the membrane of the embryo-sac curve over at the apex, and run inward on the pollen-tube. But it is quite possible that the embryo-sac, originally somewhat pressed inward by the entering pollen-tube, being of course very thin and delicate at this time, sometimes even merely of a gelatinous consistence, may become dissolved gradually from the apex of the pollen-tube, so that the latter shall actually break through it. Such a gradual solution must, at the same time, obliterate every sharply-defined border, which certainly is never seen. It may be, however, that the embryo-sac is only expanded out, so as to become very thin. The possible modifications do not appear to me to be important here, since by the subsequent construction the embryonal vesicle comes also to lie in the cavity of the embryo-sac, and of course, after cell-formation begins, not merely any possible coating of membrane of the embryo-sac, but also the pollen-tube itself, disappears from observation (becomes absorbed). With regard to that, I may remark that the transformation of the germinal vesicle into the embryonal globule by the formation of cells within

* Flora, 1844 and 1845, p. 193.
† Flora, 1845, pp. 787. and 593. et seq.

cells may always be easily observed. Usually one of the new cells fills up the whole vesicle, and the rest are formed in the suspensor. Sometimes (?) several cells combine, simultaneously, to fill the germinal vesicle. Meyen himself has given most beautiful evidences of this in his plates, e. g. *Physiologie*, vol. iii. Pl. XIII. fig. 42., the free cytoblasts in the germinal vesicle; fig. 43. the young cells with their cytoblasts; fig. 35., in the uppermost cell of the germinal vescicle, two free cells with their cytoblasts; figs. 11. and 14., free cells with cytoblasts in the germinal vesicle. Two other peculiar conditions must also be discussed here. Not unfrequently the pollen-tube swells up before its entry into the embryo-sac (in *Ceratophyllum*, *Taxus*, *Juniperus*), and this expansion, lying in the parenchyma of the nucleus, or in the micropyle canal, becomes likewise filled with cells, and remains thus perceptible for a long time (in *Cynanchum*). In other plants, on the contrary, especially in the *Naiadaceæ* and *Scitamineæ*, the pollen-tube forms an expansion inside the embryo-sac, which sometimes resembles a somewhat flattened globule (in *Potamogeton*, *Maranta*, *Statice*), sometimes is a longish cylindrical body (in *Tropæolum*): in the first case the pollen-tube then elongates from the summit of the globule; in the second, from the side of the cylinder, into a prolongation of various length, and then first swells up to form the germinal vesicle. That expansion also in the interior of the embryo-sac, beneath the germinal vesicle, in general becomes filled with cells, and then remains long perceptible. In *Tropæolum*, by simultaneous absorption of the investing portion of the integuments of the seed-bud, it even comes to lie free in the cavity of the germen, and grows independently, as a cellular cord, quite round the seed-bud, and is indeed distinctly to be recognised on the ripe seed.

A remarkable aberration from the usual structure of the embryonal globule, as here sketched, occurs in the *Coniferæ;* but the investigation of these requires so much skill, patience, and perseverance, that I dare not declare myself content with the year's research I have applied to them. What I have observed is as follows; and I here beg the reader to recall correctly to recollection the description given above of the seed-bud of the *Coniferæ*. The pollen-granules here, of course, arrive immediately upon the naked seed-bud, and from the width of the micropyle usually at once upon the papilla of the nucleus. Here they lie for a variable time, then gradually emit tubes which grow through the parenchyma in various places. Thus they reach the situations where merely the membrane of the embryo-sac covers the enlarged cells of the endosperm, and penetrate into these, quite filling them up. On the commencement of this last process no doubt can prevail in the abundance of examples of almost all our indigenous *Coniferæ*. In *Abies excelsa*, *Taxus baccata*, *Juniperus sabina*, I succeeded in dissecting out the entire pollen-tube from the papilla of the nucleus to the bottom of the little hole, with the expanded portion accurately filling this. During this process, beneath the said enlarged cells (*corpuscula*, R. Brown) extends downward to the chalaza a gradual solution and absorption of the parenchyma previously formed here, whereby is formed a cylindrical cavity beneath each of those cells, and only separated from it by the epithelium-like layer of cells which surrounds it. Into this cylindrical cavity the pollen-tube now penetrates, breaking through the wall of the little hole; but I have only twice succeeded, in *Taxus* and *Juniperus*, in dissecting out the pollen-tube in unbroken continuity, and here, also, after it had penetrated a little distance into this cylindrical cavity. My further observations are still

quite imperfect. They show that in those parts of the pollen-tubes which have penetrated into the cylindrical cavity, a process of cell-formation soon begins, so that four cells are formed, which, parallel to the pollen-tube and to each other, extend in a cylindrical form; then in the free extremity of each another cell is formed (*Juniperus communis*), which soon developes into three (?) cells (*Abies excelsa*), so that the embryonal globule now consists of twelve cells placed side by side in four rows. The process of multiplication of the cells then advances, and a little papillose, cellular body is formed as embryonal globule, which is seated on a long suspensor composed of four parallel cells. The cells of the latter continue for a long time to expand exclusively in length, and thus acquire a tortuous condition in the too short cylindrical cavity. At the place where they come forth from the large cells (*corpuscula*), some cells also appear to be formed sometimes, or the neighbouring cells compress the cavity of the pollen-tube together; in short, there is very soon no further trace of the originally free communication to be discovered.

Special deviations besides so mentioned I have not yet met with, nor is it probable that differences should occur in the essential particulars when it is remembered that the peculiarities which distinguish the *Cryptogamia*, *Rhizocarpeæ*, and *Phanerogamia* are far greater than the main points which appear to occur throughout the whole animal kingdom; yet the *Phanerogamia* agree so closely in all the rest of their organisation, that it is very improbable that they should exhibit important modifications in so essential a point. In the Plate IV. of this volume I have given a series of the most instructive, and easiest to repeat, observations; especially in *Epilobium angustifolium*, *Orchis latifolia* and *Morio*, *Martynia diandra*, *Salvia bicolor*, *Œnothera rhizocarpa*, *acaulis*, and *Momordica Elaterium*. I will only add a few words on the preparation of such dissections. If the seed-buds are not very closely enveloped, and immoveable in the germen, I extract them, take them between the thumb and fore-finger in such a manner that with a sharp razor I can cut them accurately in half. To obtain these halves symmetrical, and that the section may hit the micropyle canal, or come near enough to it, I place the seed-bud in the proper position between the fingers, if necessary, with a lens. The two halves thus obtained I place one behind the other, the cut surfaces toward the thumb, between the thumb and finger again, and cut with the razor the thinnest possible slice from the surfaces of the sections. I then bring these two slices under the simple microscope, and dissect the parts with fine needles and knives, if they are not already made evident by the section, which is of course always the best. In one-seeded germens the same may be done if they are very small; in other cases I at once cut as fine slices as possible, e. g., in the Gourd.

It is evident that one must always previously study the structure of the unimpregnated seed-bud and germen, and the form of the pollen-tube, and by careful observation make oneself acquainted with the periods of fecundation. Patience and perseverance will always have to be applied as the most important of all means of success. A hundred such slices as I have described may often be made and nothing seen, and perhaps the hundred and first will be so good as at once to complete the investigation. I do not think the method of dissecting off the parts of the seed-bud from without inward, under the simple microscope, advantageous, because much more is destroyed, and in particular displaced, in this than in one simple section made with a sharp instrument.

*History.*

We not unfrequently find examples in Science, of the unprejudiced glance of the first observer divining and expressing the truth, which, however, is naturally at once thrown aside by Science as unfounded and contradicting its temporary laws, till in the end it works back gradually to that first notion, but now consciously, and supported in every way by the true reasons. Thus, if we look to the result now secured as to the origin of the embryo, it is at the bottom exactly the same as that which was asserted more than a hundred years ago by Samuel Morland *, namely, that the pollen-tube descended through the style into the seed-bud and became the embryo. This notion, in its crude form, was contested, and, indeed, at that time, properly, by Vaillant and Patrick Blair. After that, all deeper investigation, such as had been roused by Malpighi, gradually fell asleep; and when Treviranus † wrote his work on the Development of the Embryo, it was to be considered as a great advance, although he did not go beyond what Malpighi had done, and even did not reach many of the beautiful observations of Malpighi, e. g., the existence of the embryo-sac. The observation of the embryo in its earlier conditions, as the embryonal globule, from which Malpighi and Treviranus started, commenced with Ad. Brongniart (*l. c.*), and he very nearly completed the matter; if he had only used the observations of Robert Brown, which soon followed, and by means of these explained his observations on *Momordica Elaterium*, which only wanted an intermediate stage, easily added hypothetically, he would have discovered the origin of the embryo from the pollen tube penetrating into the embryo-sac. Thus the materials stood till I ‡ brought the matter to a conclusion by my researches. I regard it as wholly superfluous to report on the many opinions of those whose imagination was busier in spinning out their own discoveries, than their hands in dissecting or their eyes in observing accurately — people who in all ages have confused natural science instead of advancing it.

### *B.* THE DEVELOPMENT OF THE EMBRYONAL GLOBULE INTO THE EMBRYO.

§ 166. The main features of this section have necessarily been already given (§ 121.), but this is the place in which to enter into this matter somewhat more specifically; for this purpose it seems requisite to separate the Monocotyledons from the Dicotyledons, and the Gymnosperms from both. As an universal law, valid for all *Phanerogamia*, there is only one thing to be expressed, that the part of the embryonal globule corresponding to the point of the pollen-tube always becomes the bud; the opposite part therefore, of course, that turned toward the apex of the embryo-sac, the nuclear papilla and micropyle, becomes the radicle. The existence of this law of position of the radicle in the seed-bud was first stated by Robert Brown.

* New Observations on the Parts and Use of the Flower in Plants. Phil. Trans., 1703.

† Von der Entwick. des Embryo, &c. Berlin, 1815.

‡ Einige Blicke auf die Entwickl. des veg. Organismus, Wiegmann's Archiv, 1837, vol. i. p. 289.; Ueber Bildung des Eichens und Entstehung des Embryo, Act. Acad. C. L. C. vol. xix. p. 1.

§ 167. 1. *Gymnosperms.*— The process of cell-formation by which the embryonal globule is produced continues on, but in very different forms, in different parts of the embryo. The apex of this has acquired, through twelve cells originally formed, a definite form and determinate limits externally, and retains these. At first this end is bluntly rounded off, subsequently from two to twelve foliaceous organs originate (in such a manner that the extreme point always remains free) simultaneously and in a circle; in the earliest condition as minute papillæ, standing on the border of the upper convex surface, gradually, however, growing up beyond the point (which always remains free), and then by degrees covering it up by applying themselves more closely together over it: these are the cotyledons or germ-leaves. Very different phenomena are exhibited at the other end: there the process of cell-formation is apparently continued still further on in the suspensor. The extreme cells formed here always become at once more or less elongated, at a somewhat later period curve away from one another, so that the end of the embryo, the radicle, never has a definite boundary, but appears to lose itself among very lax cells. This condition persists until the full development of the embryo, which always passes, through these cells, which constantly appear more lax, almost at once into the four long cells of the suspensor, which remains unchanged to the time of maturation of the seed. The very long suspensor is, moreover, gradually compressed into a coil by the growing onward of the embryo; it may, however, be disentangled, even in the ripe seed, with some care.

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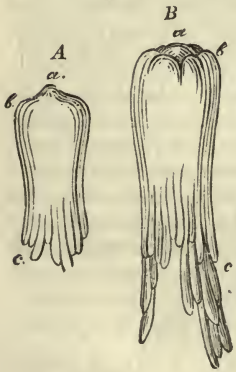


The preceding exposition is from my own researches in our native *Coniferæ*. From the beautiful analyses of the ripe seed of the *Cycadaceæ* by L. C. Richard *, as well as from the miserable figures by Gaudichaud †, it is certainly similar in this family also, with the distinction that here occur constantly only two cotyledons, which are blended up to the free points, and only leave a slit on one side for the subsequent protrusion of the enclosed bud. In *Viscum* also, according to the excellent researches of De Caisne ‡, something similar seems to occur in reference to the formation of the radicle. This want of a definite limitation of the radicle essentially distinguishes, so far as I know, the Gymnosporous from all Mono- and Dicotyledonous plants, in which I have never found any thing similar.

* Commentatio Botanica de Coniferis et Cycadeis, opus posthumum ab Achille Richard in lucem editum. Stuttgardt, 1826.

† Rech. Gén. sur l'Organogr. &c. Paris, 1841.

‡ Mém. sur le Dev. du Pollen, de l'Ovule et sur la Structure des Tiges du Gui. Brussels, 1840.

253 *Abies balsaminea: A*, Embryo in a very young condition: *a*, terminal point of the axis, the future terminal bud; *b*, border from which the cotyledons subsequently arise;

§ 168. 2. *Monocotyledons.*—In all the plants of this group which I have hitherto examined, the embryonal globule, originating in the way above described, is definitely bounded in its entire circumference; where a striking suspensor exists, the apex of the radicle, which has its outline clearly marked, projects into the cavity of the utricle, the remnant of the pollen-tube which is applied around it. Its form varies, sometimes globular, sometimes ovate, with the narrower end turned, as radicle, towards the micropyle. By the constant operation of the process of cell-formation, it grows, and is composed of successively more numerous and smaller cells. In the *Orchidaceæ* alone it persists in the earliest condition until the ripening of the seed and germination; in all other plants yet investigated, a cotyledon is formed in the following manner. Somewhat laterally to the apex of the embryo (therefore somewhat below it), a little papilla arises; from the base of this papilla a greater amount of the periphery is gradually included as part of the elevation, till at last a leaflet is formed surrounding the apex (terminal bud) with its base. The terminal bud (*plumule*) then projects like a papilla from the sheath of this leaf, the margins of which (constantly lower from the axis of the leaf toward the angles) are in contact. Thus far the development of all embryos which I have investigated is exactly similar, at most differing in the fact that the portion of the embryo in the lower half of the cotyledon sometimes attains a very considerable size about this time, sometimes merely forms the lower end of the embryo, in the shape of a cone rounded off at the apex. All the further, in outward appearances such great variations of Monocotyledonous embryos, are dependant on the unequal development of these parts, which are all alike in the rudimentary condition of the radicle (*Naiadeæ* and some other families, which L. C. Richard named *embryons macropodes*) or of the cotyledon (in *Scheuchzeria*, most *Araceæ*), &c.

In spite of the apparently great variation of the embryo in Monocotyledonous plants, the manifold forms all start from one element, and have the main point of the development in common. The earliest rudiment here, as in the Dicotyledons, the embryonal globule, developes no further up to the period of germination in the *Orchidaceæ* (fig. 254.). In all others the changes above mentioned manifest themselves, and a few examples may illustrate the statement, for which purpose the embryo of *Potamogeton*

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*c*, the radical extremity, lost in loose cells. *B*, A somewhat later condition, in which the individual cotyledons are already distinctly recognisable: *a*, *b*, *c*, as in *A*.

254 *Neottia picta.* Ovate embryo, without a cotyledon.

255 *Potamogeton lucens.* *A*, Embryo: *a*, radicle; *b*, cotyledon. *B*, Longitudinal section of the same: *a*, *b*, as in *A*; *c*, slit of the cotyledon, with the plumule.

(fig. 255.), with a strikingly developed radical extremity (fig. 255. *a.*), and the embryo of *Scheuchzeria* (fig. 256.), with a predominantly developed cotyledon (fig. 256, *b.*), appear best fitted. If the radicle is destined to be little or not at all developed subsequently in germination, there are formed already at this period, from the place where the cotyledon is connected with the bud (as the first node of the plant), adventitious roots, which, in the embryonal condition, still remain inside the parenchyma of the true root (fig. 257, *b d.*), as in *Lemna*, *Pistia*, *Gramineæ*,

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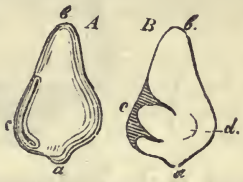


*Scitamineæ.* The vaginal portion of the cotyledon may likewise become more or less developed, and wholly, partly, or not at all enclose the terminal bud: in the first case, the borders of the sheath always become blended, so as to leave only a large (*Araceæ*, 257. *A. c. B. c.*) or small (*Liliaceæ*) slit, which, however, is, in all instances, still perceptible on the ripe embryo; in the second case, the bud partly projects out from the slit, e. g., *Scheuchzeria*, some species of *Pothos*, &c.; the last case, which is the rarest, occurs in *Stratiotes*, *Aponogeton* (fig. 258, *c.*), *Ouviranda*, *Orontium aquaticum*, &c. The forms of these individual parts are also very various, as in general the organs of plants are not bound down to any particular form. Sometimes the cotyledons are developed broad, obconical, on the little conical papilla, e. g., *Pothos reflexa* (fig. 260.), sometimes umbrella-shaped, or like an Agaric-pileus, as in the *Cyperaceæ* (fig. 259.); sometimes even like a hollow cup,

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[256] *Scheuchzeria palustris.* *A*, Longitudinal section of the embryo: *a*, radicle; *b*, cotyledon; *c*, slit of the same, with the plumule.

[257] *Pistia obovata.* *A*, Embryo: *a*, radicle; *b*, cotyledon; *c*, slit of the same. *B*, Longitudinal section of the embryo: *a*, *b*, as in *A*; *c*, slit of the cotyledon, with the very simple plumule; *d*, adventitious root.

[258] *Aponogeton distachyon.* Embryo. *a*, Radicle; *b*, cotyledon; *c*, free plumule.

[259] *Isolepis supina.* Longitudinal section of an embryo. *a*, Radicle; *b*, cotyledon; *c*, plumule covered by a sheath from cotyledon, and directed downward.

[260] *Pothos reflexa.* Longitudinal section of an embryo. *a*, Radicle; *b*, cotyledon; *c*, its slit, with the plumule; *x*, doubtful second bud.

containing the small quantity of albumen which exists in its cavity, as in *Orontium aquaticum* (fig. 262.). The radicle is sometimes simply roundly apiculate, sometimes elongate-cylindrical, and then suddenly truncated into a surface occasionally umbilicate in the centre, e. g., *Potamogeton* (fig. 255.), &c.; sometimes very thick, flat below and attenuated above, as it passes into the cotyledon so that the embryo represents an erect cone (in many Palms, fig. 261.). All these anomalies are

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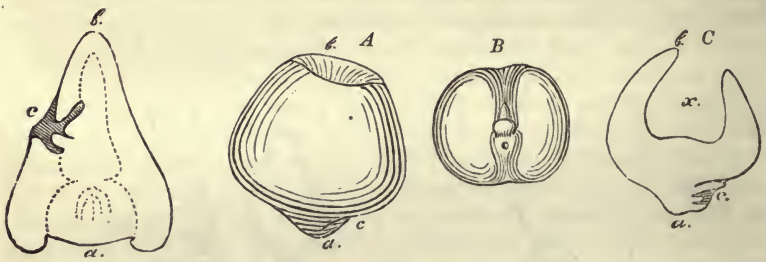


easily traced to the fundamental type through the progressive development.

In most of the cases hitherto named, the position of the terminal bud on the ripe embryo is not at all unnatural. Originally occupying the apex of the embryo, it often appears lateral on account of the great mass of the cotyledon, forming an angle with the axis of the latter; sometimes, however, the cotyledon is so strongly developed that it forms a right angle with its axis (fig. 257.), consequently also with the axis of the radicle, which usually appears as a direct prolongation of the cotyledon. The structure in *Lemnaceæ* is apparently the most aberrant (fig. 263.); here the ripe embryo is a large, longish, conical, or ovate mass; below, at the thicker end, which is turned toward the micropyle, therefore on that account already to be determined as the radical end, a very small transverse slit is exhibited. If a cross section is made through the embryo here, we see that behind this slit the bud, consisting of a flattish rudiment of the stem, lies in such a direction that its axis is almost parallel with that of the cotyledon, and its apex also directed toward the micropyle (fig. 263, *C. c.*); on the other side of the radical

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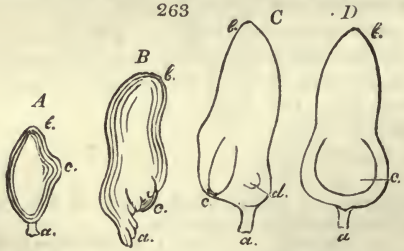


261 *Chamædorea schiedeana.* Embryo in longitudinal section. *a*, Radicle; *b*, cotyledon; *c*, slit with the plumule.

262 *Orontium aquaticum.* *A*, Embryo: *a*, radicle; *b*, cup-shaped cotyledon; *c*, free plumule. *B*, The same seen from beneath: *c*, the point of attachment of the funiculus (hilum). *C*, Longitudinal section of the same: *a*, *b*, *c*, as in *A*; *x*, the cavity of the cup-shaped cotyledon.

263 *Lemna gibba.* *A*, Very young embryo: *a*, radicle with the torn suspensor; *b*, co-

end we then discover, in this transverse section, an adventitious root (fig. 263, *C. d.*) still buried in the parenchyma, but already perfectly determined, and even provided with a *calyptra ;* this, also nearly parallel with the axis of the embryo, has its apex turned toward the micropyle ; the axes of the bud and the adventitious root form an angle of scarcely 30° with their divergent apices. If we trace the development we see that the bud originally forms the apex of the embryo, and is afterwards gradually thus pushed aside by the growth of the cotyledon. The course of development (which is analogous to that of *Cyperaceæ*) I have traced so often in *Lemna minor* and *trisulca*, as well as in *Telmatophace gibba*, investigated so many ripe seeds of the three said plants, and of *Wolffia Delili*, that I may venture to declare that nothing at all corresponding, even distantly, to the analysis given by A. Brongniart* occurs in the embryo of the *Lemnaceæ ;* how he obtained such strange figures I cannot explain.

The import of the individual parts of the embryo of Grasses, which formerly gave botanists so much trouble, is exhibited most simply in the course of development. In the Grasses the embryo is originally formed exactly as in other Monocotyledons (fig. 264, *A.*); but the following variations subsequently appear. During the formation of the vaginal portion the bud is also considerably developed, and thus that part of the vagina covering it is pushed outward (fig. 264, *B.*), and a papilliform process is gradually formed over the bud, becoming blended, leaving only a slit: this process is usually regarded as the free bud, not enclosed by the cotyledon (fig. 264, *C. e. f.*). But if this part †

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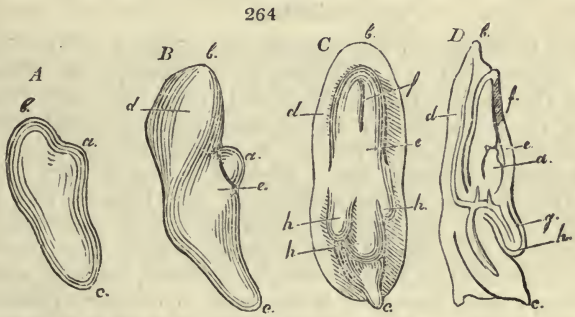


* Arch. de Botanique, vol. ii. p. 97. (1833.)

† Some name it with the superfluous term *Coleoptile.*

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tyledon ; *c*, plumule. *B*; Later condition: *a, b, c*, as in *A*. The radicle is not yet completely rounded ; the suspensor is removed ; the plumule is already partly enclosed in the sheath of the cotyledon, and pushed downward. *C*, Perfect embryo in longitudinal section: *a, b, c*, as in *B ; d*, rudiment of an adventitious root. *D*, Perfect embryo in longitudinal section at right angles to the preceding: *a, b, c*, as in *B*.

[164] *Secale cereale.* *A*, Very young embryo: *a*, rudimentary plumule; *b*, cotyledon ; *c*, radicle. *B*, Later condition: *a, b, c*, as in *A ; d*, the expansion of the *scutellum* beginning ; *e*, commencement of the formation of the vagina of the cotyledon, which envelopes the plumule. *C*, Perfect embryo (not so much magnified as in *A* and *B*): *b, c*, as in *B ; d*, cotyledon as *scutellum ; e*, vaginal part of the cotyledon ; *f*, slit of the same ; *h, h, h*, adventitious roots, still enclosed in the cortical portion. *D*, Longitudinal section of the former: *a—f*, as in *B* and *C ; g*, adventitious root ; *h*, investment of it formed by the cortical substance.

is now compared with the developed leaf, we find that it exactly corresponds to the ligule. The cotyledon itself is also developed strangely, expanding out as a flat lamina, not only upward and laterally, but also downward (fig. 264, *C. b. d.*). Thus is formed the so-called *scutellum*, to which, on account of its freely projecting bud, covered with an investment from the vagina, and its equally projecting radicle (fig. 264, *c.*), the embryo appears to be adherent. The radical extremity is finally perfected to a little cone; as, however, it is never to be developed, the rudiments of several adventitious roots (fig. 264, *h.*) are formed from the base of the bud, at the point where it is connected with the cotyledon, therefore from the first node of the plant: these then, lying on the parenchyma of the radicle, appear to be surrounded by a sheath* (fig. 264, *D. h.*), the true radicle. Then, in addition, it often happens that the cotyledon arises into a kind of collar on both sides of the bud and radicle, and thus more or less completely encloses them again, e. g., in *Zea Mays*, which has been very incorrectly compared with the true slit of the cotyledon.

On the whole, abnormal modes of development of the embryo do not appear to occur in such numbers in the Dicotyledons as in the Monocotyledons; the family of the *Orontiaceæ* especially certainly furnishes wonderfully rich material for the discovery of most interesting facts; the forms of the embryos perfectly agree scarcely in any two species of *Pothos*, and, if I am not very much mistaken, embryos with two or three buds occur, e. g., in *Pothos reflexa* (fig. 260.): on this point, however, my knowledge of the development is too imperfect for me to venture to speak.

### *History.*

The first to whom we owe minute investigation of the Monocotyledonous embryo, was C. L. Richard, in his Analyse du Fruit, 1808; soon after that Robert Brown discovered (Prodr. flor. nov. Holl. 1810) the slit of the cotyledons in the *Araceæ*, *Typhaceæ*, and *Naiadaceæ*; he looked upon this, however, as a peculiarity of these families, and all botanists followed him. Mirbel †, in 1829, very indefinitely indicated an analogy of the embryo of the Grasses and *Liliaceæ*. Finally, in 1837, I ‡ demonstrated, from the history of development of a great number of Monocotyledonous embryos, not only that the slit of the cotyledon, discovered by Rob. Brown, is universal, but also showed that it must always exist, because it is the result of the true typical development of the embryo. These observations were soon afterwards confirmed by Ad. de Jussieu § in an interesting treatise, and the analyses of some rarer and very aberrant embryos added. All that Link (El. Phil. Bot.) says about the embryo is wholly worthless, because he evidently has not observed the course of development of *a single one* himself, and therefore arbitrarily guesses at random of the individual parts of the ripe embryo.

§ 169. 3. *Dicotyledons.*—The embryonal globule in the Dicotyledons has sometimes rather a spherical and sometimes rather an ovate form. I cannot decide whether it retains this form until the

* Some therefore call the true radicle the root-envelope (*coleorhiza*), which is altogether superfluous.

† Mém. de l'Acad. des Sc. 1836, p. 646.

‡ Wiegm. Archiv. 1837, and A. L. C. N. C. vol. xix. p. 1.

§ Sur les Embryons Monoc. Ann. des. Sc. Nat. June, 1839.

ripening of the seed, because I have not been able to pursue the development in those plants to which undivided embryos are usually ascribed (*Bertholetia* and *Lecythis*). Wherever I have been able to follow this out, I have found the formation of the cotyledons which I am about to describe; the genus *Cuscuta* alone forming an exception to this. In these plants the embryonal globule grows into a longish stem, without *any trace* of foliar organs except in the (single?) case of *Cuscuta monogyna.* In all the remaining cases which I have hitherto been able to investigate, there are formed on the embryonal globule, sometimes leaving free a considerable part of the point in a papillary form, sometimes only a small part of it extending to a few cells, but never occupying the extreme point, two leaves, at first as little lateral papillæ, which gradually extend on both sides, embracing between them, with their bases, the point of the embryo as a free bud. This is also considerably developed, and produces sometimes more, sometimes fewer, or occasionally no leaves at all in the embryonal condition. Here, again, the varieties of the perfect embryo depend upon the varied ulterior developments of the individual parts thus formed in a rudimentary condition.

Sometimes the radical end is disproportionately developed, as in the *Pekea* and *Rhizophora;* sometimes the cotyledons; occasionally, but not frequently, one cotyledon alone is greatly increased, whilst the other makes no advance in growth; this is the case with *Trapa natans,* in which I have observed, in an early condition, a large papilliform terminal bud, and at the sides two equal-sized cotyledons (?); but I have not been able hitherto, notwithstanding every pains, to discover the intermediate stages between this state and that of the ripe seed.

Of a large series of interesting conditions, which were in great part observed by Bernhardi (Linnæa, Bd. vii. § 572.) in germinating plants, we have unfortunately no history of the development of the embryo. All that is commonly said on that subject is merely idle, useless speculation, more calculated to mislead than to enlighten. The cotyledons may be blended, as often occurs; and cotyledons originally equal may be subsequently unequally developed. Future minute researches can alone solve the problem here.

### *C.* DEVELOPMENT OF THE GERMEN AND SEED-BUD TO FRUIT AND SEED.

§ 170. During the development of the embryo, cellular tissue, if not already existing, is always formed in the embryo-sac, always growing from the walls as well as from the surface of the nascent embryo into the cavity: this is called *endosperm.* How far this new cellular formation may be carried, how soon and to what extent it may be again displaced by growth of the embryo, vary extremely; but they are usually constant in each particular family. Thus a considerable portion of this endosperm is still to be recognised in the ripe seed in the *Liliaceæ,* Palms, *Gramineæ,* and *Cype-*

*raceæ* amongst the Monocotyledons, and in the *Ranunculaceæ, Papaveraceæ, Umbelliferæ* amongst the Dicotyledons, &c. Even where the embryo-sac is very narrow, such an endosperm is often to be detected in the vicinity of the embryo, as, for instance, in the *Nymphæaceæ* and the *Hydropeltideæ*. Very rarely indeed, and, so far as I yet know, only in the *Cocoineæ* among the Palms, the process of cell-formation, starting from the walls of the embryo-sac, forms only a thicker or thinner lining to the cavity, while this is not occupied by the embryo, which is relatively exceedingly small. The cavity in this case still contains, even in the ripe seed, the formative fluid (*cytoblastema*), together with cell-nuclei and some free cells. This fluid is the so-called milk of the cocoa-nut.

The ulterior development of the new cellular tissue varies much, sometimes the walls are completely converted into cellulose, sometimes they remain in a condition which is at least very little removed from gelatine (as in the species of *Cassia*), or form various intermediate conditions between this, amyloid and cellulose, which in the dry seed are commonly called horny. The cell-walls sometimes remain quite thin, sometimes they become porously thickened in various ways: their contents are the usual contents of cells—assimilated vegetable matter, in which frequently some one constituent particularly preponderates, as oil, starch, &c. Very rarely crystals of oxalate of lime are found in the endosperm (as in *Pothos rubricaulis*).

As has been already remarked, the embryo-sac, in its formation, sometimes displaces a greater and sometimes a smaller portion of the nucleus. When a portion remains, two conditions may be distinguished according to the form of the seed-bud. In nuclei with straight axes the embryo-sac grows more or less through the axis of the same, and it is then surrounded by the remaining portion of the nucleus (as in *Nymphæaceæ, Hydropeltideæ,* and *Piperaceæ*): on the other hand, where the axes of the nuclei are curved, the embryo-sac only displaces that part of the nucleus corresponding to the circumference of the seed-bud, and its persistent part is embraced in annular form by the embryo-sac (as in the *Portulaceæ, Caryophyllaceæ*, &c.) This persistent part of the nucleus is termed *perisperm:* it consists, so far as I know, only of perfectly developed, thin-walled cells, the contents of which are amylaceous or watery, or consist of the usual assimilated matter.

In *Canna* alone the peculiarity exists that the nucleus is very early displaced by the embryo-sac, but the substance of the chalaza remains as perisperm.

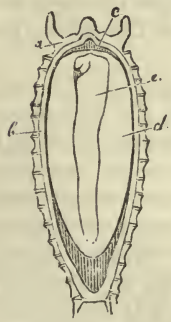
All these masses of cellular tissue are called in descriptive botany, without regard to the manner of their origin, *albumen.*

The study of development which arose with the intelligent Italian Malpighi was soon lost in oblivion. Treviranus again revived it, but did not arrive at the recognition of its profound importance as the principle of the whole science. Robert Brown was the first to demonstrate how, in all matters connected with plants, the history of development

alone can lead to the comprehension of the nature of the plant, and therefore of scientific Botany; and he it was, especially, who made the first step towards bringing light and order into the theory of the albumen. botanists have allowed it to be told them, and follow the old systems as before. In 1825, Robert Brown showed that two things totally different from each other were confounded together under the term albumen, and demonstrated their simultaneous presence in the *Nymphæaceæ*. Eighteen years have passed since that, and not a single botanist has contributed any thing to the further development of the subject. Before and after they have talked at random about the nature of things, but investigated nothing; and the treatises given by Mirbel and Brongniart in 1829–30 have been passed over without a trace: and we always find that in the most recent works of renowned botanists, *Nymphæaceæ*, &c. are described as Monocotyledons, and the albumen is mentioned without any reference to its origin. My friend Vogel (who too early fell a sacrifice to his zeal for science), with myself, endeavoured, in a memoir on the albumen*, to bring light and order into this subject. In the paragraphs I have given the essential portion of our results: many specialities are also unfolded in that essay, in which we have demonstrated, in an extensive treatise on the albumen of the *Leguminosæ*, that this is a true endosperm, and not, as DeCandolle thought, a thickened inner integument.

The important conditions may be seen by comparing together the seed of *Typha* (fig. 265.), where endosperm alone is present; of *Saponaria*, (fig. 266.), where only perisperm exists; and of *Nymphæa* (fig. 267.), where both occur simultaneously.

265

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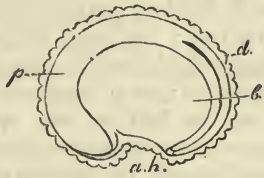


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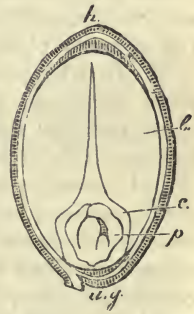


§ 171. The integuments of the seed-bud, in which I here include the nuclear membrane, are also very variable in their ulterior development. Sometimes, but extremely rarely, they become wholly

* Act. Acad. L. C. N. C. vol. xix. pt. ii. I here remark, since the usual title notice of the time of sending in has been omitted by the Editor, that this essay was sent in and received for printing by the Editor in 1838.

265 *Typha latifolia.* Fruit in longitudinal section. *a*, Integument of the fruit; *b*, integument of the seed; *c*, operculum; *d*, endosperm; *e*, embryo.

266 *Saponaria officinalis.* Seed in longitudinal section. *a*, *h*, Hilum and chalaza; *d*, coat of the seed; *b*, perisperm; *f*, embryo.

267 *Nymphæa alba.* Seed in longitudinal section. *a*, *g*, Hilum and micropyle; *h*, chalaza; *d*, seed-coat and its epidermis; *b*, perisperm; *c*, endosperm; *f*, embryo.

absorbed, at least on the outer side, by the pressure of the growing endosperm, so that the endosperm exhibits a convex-concave form, the concavity of which receives the remaining portion within it, whilst the convex surface is quite naked. This remarkable process takes place in that section of the species of *Veronica* which has been named *cochlidiospermæ*.

More frequently the integuments remain, at least as a thin pellicle, readily falling into shreds, but adhering to the endosperm, as in many *Rubiaceæ*, especially in the Coffee. Usually they form a closed envelope to the perisperm, endosperm, or embryo, according as those parts are present, and they are then termed the seed-coat (*episperm*). Its cellular tissue gradually produces more or fewer (one to five) layers of cells, developed in various ways. Frequently the entire integument appears as a very thin membrane, especially in one-sided, indehiscent fruits (as in the Grasses). We can usually distinguish several layers. Nothing general can be stated respecting the tracing back of these cellular layers to the integuments or thin parts from which they originate; the history of development of individual families, and even genera, must declare it for each separately.

In the perfecting of the seed-bud, new vascular bundles are frequently produced in the parenchyma of the single or of the outer integument, in connection with the termination of the vessels of the funiculus, usually running out in elegant radiate forms from it (as in the Hazel Nut, Lemon, &c.). The vascular bundle of the raphe alone is often so prolonged, that it runs simple through the entire circumference of the seed-bud until it reaches the micropyle (as in many *Compositæ*).

It often happens that individual parts of the integument become more developed than the rest; and here belong, in the first place, those peculiar appendages of the raphe already spoken of, which become still further developed; or a new excrescence is now produced, usually only from a fold of the epidermis, which now developes into two, rarely three usually vertical lines, into a membranous border or wing all round the seed (*ala*), or elevated ridges, rising in various ways from the surface of the seed, and, if reticularly connected, often forming little pits between them (as in *Scrophulariaceæ*). Again, the exostome sometimes produces a peculiar appendage in the form of a papilla (*Euphorbiaceæ*), or a tuft of hair (*coma*) grows out (as in *Asclepiadaceæ* and others), or forms a cup-like excavation with a fringed edge (as in *Philadelphus*), &c. In the region of the chalaza, also, peculiar modifications of the cells are often exhibited, appearing as papillæ, gibbosities, and the like, or as a variously, but often distinctly bounded colouring (as in *Abrus precatorius, Erythrina corallodendron*, &c.).*

* Link (Elem. Phil. Bot. vol. ii. p. 285.) says, very inaccurately, the umbilicus in *Abrus precatorius* is coloured black. On the umbilicus (hilum) the colour is not deep, as that only occurs on the chalaza, and in *Erythrina* does not reach the umbilicus at all.

Finally, it is to be mentioned, in some plants the endostome (as in *Lemna*), in others both the exostome and endostome (as in *Pistia*), in others, again, the whole of the integuments of the seed, which had previously formed a peculiar circular fold (as in *Maranta* and the *Commelinaceæ*), and, lastly, in *Canna*, the whole of the integuments over a small portion of the periphery of the seed-bud, which become hardened by the thickening of these cells, independently of all the rest, and easily separable from them, lie as an operculum on the radical end of the embryo, and so are termed the *operculum* or *embryotega*.

I must, alas! again repeat here, what impresses itself upon the penetrating inquirer at every step in Botany, that almost all the existing material, from the total want of scientific principles, scarcely carries us beyond the very beginning of science. Scarcely anything can be used, almost every thing is yet to be done, almost every investigation must be recommenced from the very beginning, under an improved method. A greater confusion than that which prevails in the theory of the seed-coats is scarcely conceivable. The most heterogeneous things are thrown together under one name, thoroughly identical ones placed in totally different classes of organs; and there is nothing for it, if we would not make still greater confusion, but to cut the thread altogether and begin over again. The epidermis of the seed, as I have delineated it, is described sometimes as *testa* in the *Leguminosæ* and *Drosera*, sometimes as *arillus;* seed-membranes are introduced, as in *Canna* and the *Compositæ*, where no true integuments exist. Appendages of the raphe, thickened micropyle, thickening of the funiculus, true arilli, run gaily through one another as *caruncula*, *strophiolus*, *arillus*, and under a dozen other names; every one has new names in readiness. To observe how the things are formed, what their import is in the plant, few do, and most Botanists let the few like Brongniart, Rob. Brown, Mirbel, and others lie on the shelf. One person cannot help in the matter; he can only complain, and invoke a better spirit to animate Botanists.

The whole theory has been constructed hitherto solely according to hypotheses, among which especially the view principally established by Gärtner, in his otherwise inestimable work (*de fructibus et seminibus plantarum*), takes the first rank; a view totally contradicting nature, that the seed must necessarily be covered by two coats. Whence the law is derived, how it is deduced from the nature of the plant and the seed, no one says; and yet this prejudice is so firmly adhered to, that even after the works of Rob. Brown, Brongniart, and Mirbel had appeared, very talented persons thought they settled a matter very cleverly when they said, one should not be afraid of the periphrasis, for instance, in *Viburnum*, but had best give: *spermodermis incompleta e tunica simplici formata.* I think, however, that one should not be afraid to throw away old prejudices, without any ground in profound investigation of the nature of the plant, but should say simply *epispermium simplex** ; or, for instance in *Ricinus* and *Chelidonium*, *epispermii stratum medium crustaceum*, *internum membranaceum*, whereby it at least remains undecided to which integument the layer named belongs, since in *Ricinus* the brittle (*crus-*

The umbilicus itself, i. e. the point of separation, is never especially coloured, and is only otherwise evident by the shining surface of the torn cellular tissue.

* I prefer the older name of C. L. Richard.

*taceum*) is the epidermis of the inner integument, closely connected with the parenchyma of the same, and the membranous layer of the nuclear membrane; in *Chelidonium*, on the contrary, the brittle layer is the whole external integument clothed with delicate epidermis, and the membranous layer is the inner integument. In *Ricinus*, therefore, the outer integument would come in as *stratum externum evanescens*; in *Chelidonium*, the epidermis as *stratum membranaceum medio arcte adhærens*. To make the confusion quite perfect comes next the circumstance, that the different observers, in the analysis of ripe seeds, have determined the number of coats, in dissections made according to various methods, or in transverse sections under weaker or stronger magnifying power, according to the variations of the cells quite undistinguishable in them: so that a seed has often been determined to have a simple seed-coat, which has two or three; others actually with a simple membrane, favoured with two or three seed-roots, on account of differences in the development of the cells. From the small number of observations which have as yet been published by Brongniart, Mirbel, Brown, and myself, it already follows, with perfect certainty, that every determination of the coats of the ripe seed is altogether useless, if their nature has not been demonstrated by the course of development.

The case mentioned in the beginning of the paragraphs, of the cochlidiosperms of the species of *Veronica*, has appeared to me as yet the most difficult subject of investigation, and I was obliged to take the research up several years, one after another, till I had completed it, since, in addition to all the other abnormalities, totally unsymmetrical formation of the seed-bud occurs, which renders the investigations very much more difficult.

The most general condition is where the epithelium of the external or the simple integument, or the nuclear coat, is developed in a remarkable manner. Thus, in most plants, especially those which have a hard shining seed (e. g. the *Leguminosæ*), it is converted into a tissue, composed of relatively long prismatic cells, placed perpendicularly to the surface of the seed, and usually much thickened, even to the partial obliteration of their cavities. In other plants, particularly such where the seed, when placed in water, becomes coated with gelatinous matter, it consists of cylindrical cells placed in the same manner, but with thin walls, and densely filled with gelatinous matter (Quinces, *Plantaginaceæ*), and which frequently contain elegant spiral fibres (many *Polemoniaceæ* and *Cucurbitaceæ*). Here it is often easy to observe the gradual filling of the cell with starch, the solution of this to gum, and the conversion of this into the very hygroscopic gelatine, while the spiral deposits are simultaneously formed on the wall.* More frequently that gelatine is wanting, and the cells, less cylindrical in form, project in a papillose manner as hairs, or several unite together as little spines, gibbosities, or ridges, &c., rendering the surface of the seed uneven; or they form a flat surface, while their walls are thickened by a variety of spiral, reticulate, or porous deposits (in *Hydrocharis*, most *Labiatæ*, *Solanaceæ*, *Scrophulariaceæ*). In a few cases these cells develope, in exceeding delicacy, to a large size, and become filled with fluid, so that the seed resembles a berry (in *Punica granatum*, in *Ribes* (?) ). Those cases are remarkable in which these cells expand so much in the surface that they necessarily

* See Müller's Archiv, 1838, p. 152.; and Schleiden's Beiträge zur Bot. vol. i. p. 134.

become torn from the cells beneath them, and then surround the seed as a loose sac (e. g. in *Drosera* and *Parnassia*), or, transformed in a peculiar manner into an elastic tissue, tear open and discharge the seed (in *Oxalis*). The rest of the tissue of the integument, beneath the epidermis just described, is very variously developed. Sometimes next the epidermis is a layer of looser cells, with intercellular passages or spaces (e. g. in *Leguminosæ*), into which, in the only cases, *Canna* and *Nelumbium*, where the epidermis exhibits stomates, these latter lead. We usually find next to the epidermis and firmly attached to it, a thin layer of parenchyma (the whole outer integument), and then, distinct from this, a special coat consisting of an extremely delicate layer of cells (the inner integument alone, or with the nuclear coat) : this is the case in most *Liliaceæ*.

A different formation is not unusually met with, where two integuments exist, and the inner is not formed by a mere fold of the epithelium. Here the epithelium of the inner integument is generally exactly in similar conditions to some of those generally described above, while the outer integument becomes gradually suppressed, and falls off in shreds (e. g. in *Euphorbiaceæ*), or remains as a thinner envelope (e. g. in *Cistaceæ*, *Thymelacæ*, *Lauraceæ*). Elegant spiral thickenings also occur here in the epidermis of the inner integument (*Lauraceæ*, *Sparrmannia africana* (?) and others).

The occurrence of spiral, reticulated, and porous deposit-layers in the epidermis of the seed is so usual that it is not worth while to enumerate the cases now. A very rich variety of forms is exhibited, for example, in the *Scrophulariaceæ*, especially the *Verbasceæ* and *Antirrhineæ*, but almost all the *Solanaceæ*, particularly those with a berry-fruit, exhibit sometimes true spiral fibres (e. g. *Solanum*), sometimes reticulated thickening (e. g. *Datura*). It is most remarkable, however, that this structure of the epidermis occurs extremely rarely in the seed-buds of the Monocotyledons, which almost always have two integuments, and is presented in the Dicotyledons, particularly in the *Monopetalæ*, which usually possess only one integument.

In the formation of new vascular bundles in the integuments of the seed, I have hitherto found the law almost unexceptionably confirmed, that the vessels are never distributed in the nucleus, or inner integument, but only in the outer, or the simple integument. Treviranus had previously propounded the law opposed to this, that vessels are only formed in the inner integument, because, starting from ripe seeds, he confounded the very hard and thick epidermis of many seeds with their outer integument, and the parenchyma of the same with their inner integument. Link * has the same incorrect assertion, here doubly wrong, since he distinctly refers the shell of the seed (*testa*) to the outer integument, and the inner coat (*membrana interna*) to the inner integument of the seed-bud.

That the operculum of the radicle (fig. 265. *c.*) may be formed from very different parts, follows from what has been said in the paragraphs. Mirbel first demonstrated its peculiar development in *Commelinaceæ* and *Marantaceæ;* I myself in *Canna*.

§ 172. Very important alterations take place in the funiculus also during the development of the embryo. It has been remarked

* Elem. Phil. Bot. ed. 2. vol. i. p. 285.

above, that even before the rudiment of the embryo exists, after the complete formation of the seed-bud a new structure proceeds from the funiculus, very similar to the coats of the seed-bud. But the production of such a structure is much more frequent after the formation of the embryo has begun. It is very various, according as it advances farther or is early arrested in its development (as in most *Leguminosæ*); according as the structure envelopes the whole seed as a continuous coat (in *Nymphæa, Passiflora, Taxus*), or presents itself in separate lobes and strips, here and there connected together (in *Myristica* (?)); or, lastly, consists merely of long hairs, which envelop the seed (in *Salix*): very various, according as this organ is merely membranous, or dry and fibrous (*Nymphæa, Salix*); fleshy and juicy (*Taxus*); or, lastly, becomes broken up into isolated juicy cells, which surround the seed (*Arum, Mamillaria*). In this last transformation the conducting tissue and a portion of the inner surface of the cavity of the germen usually take part. The former structures, which all have the same origin, namely, are additional developments of the funiculus, have been partly denominated by the name aril (*arillus*); the latter, where the isolated juicy cells no longer betray their origin, as pulp (*pulpa*). Particular forms, e. g. in *Salix*, are described as a *coma*.

The heterogeneous things which are usually collected under the name *arillus* pass belief, except with those who know that Botany has hitherto established its definitions almost solely on superficial impressions and external resemblances, or at best on comparisons which, from the want of sure foundations, are valueless. In Zoology the comparative method had still an import, since one organism understood as completely as possible, according to its course of development, the human, could be taken as a basis; yet the tracing of development has even asserted its right here, and the most recent researches have proved to what mistaken directions and complications mere comparisons may lead in the absence of developmental history. In Botany, on the other hand, when we do not yet understand the structure and development of a single plant completely, such a comparative method is an empty exercise of the wit. There can be no doubt that every contest is childish in which no critical tribunal, no principle for the decision, exists; that a scientific investigation is wholly vain if a principle of truth have not been previously discovered. Botany possesses nothing of the kind. Link (Elem. Phil. Bot. ed. 2. vol. ii. p. 265.) says: "At the place where the funiculus enters the seed a variously-shaped part often occurs, which has originated from the thickened and expanded funiculus, but is invested with an epidermal layer, of which the funiculus is destitute: this is called an aril. It is globular (*Euphorbia*), a cup with an entire margin (*Anagallis*), a four-toothed cup (*Polygala*), a lacerated cup (*Myristica*)." Mirbel had already shown that the gland in *Euphorbia* is totally different from an aril, and does not arise from the funiculus at all; in *Anagallis* there exists nothing bearing the most distant resemblance to an aril; in *Polygala* there is only a rather loose epidermis to the seed: and all these are thrown together by Link. Any one who calls the elastic epidermis of the seed of *Oxalis* an arillus is just as much and just as little justified as he who chooses to call it epidermis, or even pulp. The strife is

endless, Science in constant confusion and vacillation, so long as no standard exists by which to estimate the correctness of this or that opinion. Such a standard can only be found in the history of development. Organs which have like origin, like laws of development, are alike; organs of different origin, different. Forms in the perfect condition, which may occur in any part, are no characters for the distinction of organs; but only characters for their sub-division. These are the rules with which the history of development furnishes us, to define every vegetable structure with certainty. But more is required for their application than the meagre examination of a dried plant.

The formation of the aril and pulp with succulent cellular tissue is very frequent, and the occurrence of lignification is on the whole much more rare in the development of the funiculus; yet elegant spiral cells occur in the funiculi of some species of *Veronica*, and the funiculus of the species of *Magnolia* (which I have unfortunately never had an opportunity of examining) is said to consist wholly of spiral-fibrous cells.

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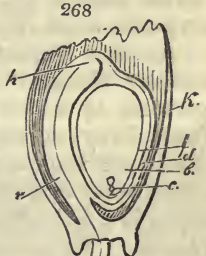



In the perfect aril, which wholly surrounds the seed-bud like an integument (fig. 268. *k.*), the closed is commonly distinguished from the unclosed: the former never occurs; where an actually closed structure surrounds the seed, it is undoubtedly a layer of the seed-coats. In the species of *Passiflora* particularly, it is always open above. Whether all the structures named in § 172, those occurring in *Evonymus* and *Myristica*, as also those in *Solanum*, belong here, I will not assert, since I am still ignorant of the history of development.*

§ 173. In conclusion, we have yet to examine the changes which take place in the germen. The germen grown to the fruit is styled the pericarp (*pericarpium*). Besides the generally considerable enlargement of the mass, which depends sometimes on the expansion of the existing cells, and sometimes on the production of new ones, we have to consider the following points:—

First, the changes in the external parts, since the pistil, as its mass enlarges, often considerably alters in the conditions of its parts. The style, in particular, is usually cast off or dried up as a part of no further use; more rarely it goes on growing, and sometimes acquires a disproportionate size, for instance, in many *Geraniaceæ*. The germen also frequently now first produces projecting ridges, warts, gibbosities, or thin membranous appendages (wings).

The conditions of the interior of the germen now become important. As in the formation of the entire pistil and of the seed-bud to fruit and seed, so, as it would appear, the development

* We have received an essay from Planchon on the *arillus* (Comptes rendus, Dec. 1844), which, from the extract published in the *Botanische Zeitung*, and his other works, awakens no especial confidence. He asserts particularly, that in *Myristica* and *Euonymus* no *arillus* occurs, but an excrescence of the micropyle, which he calls an *arillode*.

268 *Passiflora alba.* Longitudinal section of the seed. *a*, Funiculus and hilum; *h*, chalaza; *d*, external, *f*, internal layer of the testa; *b*, endosperm; *c*, embryo; *r*, raphe; *k*, aril.

of the individual parts of the pistil depend almost solely upon the healthy development of the embryo. Hence those cells in which no seed-buds are developed to seed are in like manner arrested in their development, and in the matured fruit are scarcely to be recognised. This non-development of some of the cells appears to be as it were the normal rule in some plants: thus, in many Palms, e. g. *Chamædorea*, of three cells one only is commonly developed, whilst the others dwindle away. The same occurs in all *Cupuliferæ;* and the germen of *Castanea*, with six cells and twelve seed-buds, usually produces a one-celled, one-seeded fruit. In the ripe fruit, therefore, it is always impossible to determine the original number of cells and seed-buds. On the other hand, large air-cavities are not unfrequently formed in the wall of the germen, which assume the deceptive appearance of natural cells containing no seeds, as in *Nigella.*

Another important matter, moreover, is the development of cellular tissue from the inside of the wall of the cavity of the germen, by which are not unfrequently formed, in long germens (but always subsequent to the origin of the embryo), false septa, which are transverse, and therefore have a direction in which true septa never can occur. The general term for fruits with these false septa is a *lomentum;* examples of it occur in *Raphanus* and *Ornithopus.* Sometimes this cellular tissue, instead of forming actual false septa, is accumulated thickly between and around the seeds filling the cavity, as in *Glaucium*, *Ceratonia*, &c.

The conditions of structure of the germen are here to be particularly kept in view.

Through the entire range of Phanerogamic plants, we find the most diversified metamorphoses in the structure of the germen; on account of which the ripe fruit presents a great multitude of different appearances. So far as my observations extend, two different types may be distinguished in the development, according as the layers of cellular tissue of the testa become tougher and firmer from within outwards or from without inwards. In the former, be the morphological import what it may, four several cell-layers are universally to be distinguished, although they sometimes appear more clearly than at others; namely, the epidermis of the outer surface; the epithelium of the inner surface; and between the two an external parenchymatous layer, the cells of which are generally delicate-walled, fleshy, and of simple polyhedral form; and, finally, of an inner parenchymatous layer, the cells of which are more or less thick, coriaceous, or woody, and always elongated.

The second type is exhibited in those fruits in which the parenchyma is developed more or less fleshy and succulent, and frequently toward the interior, where it bounds the fruit-cavity, broken up into isolated cells; whilst either only the epidermis of the outer surface is very thick, or else some layers of cells thicken beneath it (*Cucurbitaceæ*), or sometimes acquire even a woody texture (e. g. *Lagenaria* and *Crescentia*). In the mass of isolated, juicy cells which

often fill berries, it is no longer possible to determine how much of it belongs to the inner wall of the fruit, how much to the conducting cellular tissue and to the funiculus: the whole mass may in any case be termed pulp.

Upon the more or less distinct production of the layers of the testa, and upon their varied formation, rest all those varieties of the fruit which strike us on a first impression, and which had received their common distinctive names long before botanists had constructed fruit-systems. Where the layers are clearly distinguished, the epidermis of the surface is seldom particularly striking, the inner epithelium frequently shares the transformation of the inner parenchymatous portion, which varies in its consistence from that of leather up to a stony hardness, sufficient to give out sparks when struck by steel; but in every condition it consists of thickened cells which are usually porous. Two different conditions may be distinguished in the inner parenchymatous layer:—1st, Where several layers of cells go to its formation, the long-diameter of the cells of one layer is commonly at some angle to those of the next layer (as in *Leguminosæ*, *Amygdaleæ*, and almost all capsules); 2ndly, Where only one layer is present, the cells are so arranged that five, or six, or more cells, lying parallel, form little plates, from which the layer is so constructed, like mosaic work, that the long-diameter of the cells of one plate is never in a line with that of those of the next plate (as in *Asclepiadaceæ* and *Cruciferæ*). The epithelium of the inner surface is also sometimes changed into elegant spiral-fibrous cells, as in some *Papaveraceæ* (*Chelidonium*), in *Umbelliferæ* (*Anethum*), &c.; more rarely it is developed into true epidermis with perfect stomates (as in *Reseda*, *Passiflora*, &c.). The outer layer of parenchyma varies from a leathery consistence to the most perfect dissolution into easily compressible, succulent cells. DeCandolle and others have taken pains to trace this layer to the texture of the normal leaf. It appears to me that this is empty trifling. In the first place, it has as little of the structure of a normal leaf as of the form; secondly, many germens do not arise from foliar organs; and thirdly, in one and the same strictly-defined and quite natural family, the most essential varieties are found to exist in nearly related genera, as in the *Solanaceæ*, where true berries and capsules, and in the *Dryadeæ*, where true small berries and achænia occur.

In the formation of the berry and the pulp, the origin of cells within cells, &c., may usually be beautifully observed. The parent-cells, however, especially towards the time of the ripening of the fruit, become absorbed before the young cells are firmly united together and sufficiently expanded to become firmly connected with the neighbouring cells when they are set free; hence they remain lying loose in the abundance of juice which is simultaneously produced. A circulation in reticulated, anastomosing currents is exhibited in these isolated cells (in *Solanaceæ*, *Cactaceæ*, and *Lonicereæ*).

Some very thin-walled germens in *Araceæ* and *Naiadaceæ*, as also, in part, in those families whose one-seeded, indehiscent germens are closely united with the external integument of the seed, and thus represent what Linnæus called naked seeds (e.g. *Gramineæ*, *Labiatæ*, *Boraginaceæ*, *Compositæ*, &c.), are in the ripe fruit so compressed and so uniformly developed in all their (few) cell-layers, that they can only be classed by means of analogy with one of the types mentioned.

The epidermis of the fruit in the occasionally dehiscent fruits exhibits

cells with spiral and reticulated layers of thickening, as, for instance, in the *Labiatæ* (especially *Salviæ*), and in the *Casuarinaceæ;* and the hairs of the epidermis often exhibit the same, as in some *Compositæ* (*Senecio* and *Trichocline*), &c. The most beautiful structures of fibrous cells are formed through the entire tissue of the indehiscent germen, as in the *Compositæ* (*Picridium*) and the *Umbelliferæ* (*Sclerosciadium Prangos*).

§ 174. Similar conditions to those which occur in the bursting of the anthers and in the fall of the leaves are also presented in the fruit, and depend on the same causes, namely, the formation of layers of cellular tissue extremely thin-walled and easily destructible, which is ruptured by the slightest tension arising from the mere weight of the parts, or an unequal contraction of dissimilar layers of cellular tissue. This exists either as a peculiar layer between two differently formed masses of cellular tissue, or forms the external layer of a mass of tissue, itself having thin walls, and lying immediately in contact with some very thick-walled tissue. Whether separations of this kind shall take place, and in what particular situations, are altogether peculiarities of particular species, genera, and families, and are not dependant on any known relation to the nature of the plant. Hence solutions of continuity arise, sometimes at the place where two originally separate parts (carpels) had become blended in the suture, or else where an undivided whole originally existed *, as in the line corresponding to the mid-rib of a carpel; sometimes in the direction of the length, as in the examples which have been cited, and sometimes cutting across, as when the entire fruit falls away, or when long fruits break up into separate articulations, &c.; sometimes only in small portions of the germen, so that it opens by definite orifices. Many fruits are rent open in the most diversified manner by the always unequal drying of the pericarp, on account of the differences of the layers of which it is composed. They may open either, *a*, in individual portions, each closed in itself, and separating either lengthways or crossways (*mericarps*); or, *b*, in individual flat portions (*valves*). In the longitudinal division or the formation of valves, there remains besides these parts, in many families, a mass of cellular tissue, usually in the form of a stalk, standing in the midst of the individually separating mericarps, as in the *Umbelliferæ*, the *Euphorbiaceæ*, and *Geraniaceæ*, or of the separating valves, as in *Rhododendron*, called the columella. This is merely a separation of originally connected parts, and in none of the cases named is the remaining stalk by any means an internode of the floral axis to which the carpels were attached, but an absolutely independent cellular mass.

In very many manuals of Botany, we find directions to determine the number of carpels according to the valves of the fruit. How absurd this is, the authors might have known, from the transverse separation of the so-called circumscissile capsule and of the lomentum into separate

* Here, also, no trouble being felt about the thorough diversity, the line of separation has received the meaningless name of *suture*.

pieces, from which two facts it follows that the subsequent separation of the parts is wholly independent of the original composition. But as the word blending has hitherto been applied without any meaning, according to the arbitrary fictions of particular botanists, nothing opposed the equally arbitrary twaddle about the conditions referred to in the paragraph. The kind and manner of these separations has not the slightest connection with the original composition of the germen out of individual parts, carpels, &c., and every conclusion from the number of subsequent parts as to the number of original constituent portions merely exhibits the total unacquaintance of the concluder with the nature of plants, and of this process in particular. Here, as so frequently in the vegetable organism, in the originally homogeneous cellular tissue, which, where actual blending has taken place, becomes so closely connected that the boundary is soon wholly obliterated, layers of a very different kind of cells are developed, which exhibit great diversity, partly in the consistence of the substance forming their walls, partly in the relatively advanced condition of the deposition of thickening matter upon them. Similar cells are generally more firmly adherent to each other than to cells of a dissimilar character, and thence it happens that the different layers separate so readily, as, for instance, in the succulent part of the fruit of the Almond, Plum, Walnut, &c., from the woody. In most cases, however, thin plates of very thin-walled and speedily decaying tissue are formed for this purpose, and are lacerated by the slightest tension, and thus give rise to a solution of continuity. Even in the situations where originally distinct parts have been blended, the separation seldom (or never?) happens in such a way that the blended parts become again loosed from one another, but so that the cells are torn and destroyed; and thus, even in these cases, the circumstances of the process are by no means arrived at and expressed, when it is said that the valves are the original carpels; it is here shown, moreover, that all these solutions of continuity, in the entire plant, fall under one and the same law, that of the morphologically defined dehiscence, which is wholly different from and independent of the morphologically defined formation and connection of organs.

I will particularly cite the application which has been made of that incorrect view to the *Geraniaceæ* and *Umbelliferæ*. In these the fruit separates into distinct parts from a stalk-like mass of cellular tissue, remaining longest in connection with the summit of this, and, as it were, suspended from it. By the favourite method of guessing, this stalk is explained to be a prolongation of the floral axis, to which the carpellary leaves are attached, and from which they again separate when the fruit is mature. In the first place, it must be observed, that in the *Umbelliferæ* the whole germen is never formed of carpels, but of the axis itself. In the *Geraniaceæ*, on the contrary, there are originally five perfectly free carpels, having no trace of a prolongation of the axis between them, which become blended, and subsequently dehisce in such a manner that an internal portion of each carpel remains in the axis, while the external portion becomes gradually loosened from below upwards. The internal portion contains a liber-bundle, with the *canal of the style*. Now in the *Umbelliferæ* two little liber-bundles are found in the middle of the false septum of the germen, which remains, with a portion of their enveloping cells, in the axis of the fruit, while the two portions of the fruit in like manner tear away from them from below upward. Sometimes those liber-bundles separate from each

other from above downwards, so that the stalk-like support (carpophore) of the mericarps is bifurcately split above, or is even bipartite from the base. Dehiscences exactly similar to those of the *Geraniaceæ*, occur in all the plants in which the valves of the fruit separate from a central columella; therefore there never is *true* axial structure in these. Where, for instance, the axis (spermophore) constitutes the element, considerable portions of the carpels always remain connected with the axis, and the separation therefore equally happens within the continuity of one organ, e. g., in *Euphorbiaceæ*.

### *D.* PHENOMENA EXHIBITED IN THE REMAINING PARTS OF THE FLOWER DURING THE FORMATION OF THE FRUIT AND SEED.

§ 175. Great varieties are exhibited by the remaining parts belonging to the flower during the development of the germen to the fruit. The stamens and petals are soon after the impregnation cast off at their bases by true articulations, or they wither and die away. In rare cases a part of them remain, especially when they are blended together, and become fleshy or woody (as in *Mirabilis*). The same occurs in the perianth, but this is more frequently persistent. When the floral envelopes are partly or wholly persistent, four layers are sometimes formed in them, like the four which are exhibited in the pericarp, whilst this is only developed as a very thin membrane (as in *Elæagnus*), or they become succulent and form a false berry (as in *Morus*). The calyx, on the contrary, persists in the generality of plants until the ripening of the fruit, in which it is either little or not at all altered, as in the *Pomeæ;* or becomes large and inflated, and surrounding the fruit (as in *Physalis, Trifolium fragiferum*); or, as a *pappus*, adorns the fruit as a delicate, membranous, or hairy structure, as in the *Valerianaceæ*, the *Compositæ*, &c.; or half of it may be cast off, as in *Datura*. In many of the cases above named, these parts assume the appearance of true fruit, and this is still more frequently the case with the axial organs of the flower: thus in the Strawberry the receptacle becomes fleshy, and appears as fruit; in *Hovenia, Semecarpus*, and *Anacardium* the pedicel becomes transformed into an apparent fruit of similar nature. Most frequently, however, it is the concave disc of the peduncle which, becoming fleshy, is developed to what is vulgularly called fruit, as in *Rosa, Malus, Pyrus, Ficus*, &c. Finally, it is to be observed, that, especially in flowers without floral envelopes, the bracts and bracteoles grow with the fruit, become woody, and so form false pericarps, as in the *Cupuliferæ* the so-called *cupula*, and in *Betulineæ* the scales of the catkin.

I have here merely remarked the existence of the conditions named, since I must return to them when I come to the more minute treatment of the theory of the fruit. As in all other parts of our science, so also with respect to the fruit, we feel the want of scientific definitions; and a logical arrangement of the characters met with is nowhere less to be thought of than here. When the peasant talks of the edible part of the

Fig as the fruit, we have nothing to object; but if the botanist assumes the peasant's style of discrimination, he is far below the peasant: his science should have taught him that edibility is no test of a part being fruit. With the inconsistency thus introduced, a portion of those conditions mentioned in the paragraph have been enumerated amongst fruits according to common notions, while, in regard to another portion, it has been correctly noticed that the fruit is surrounded with another part not belonging to it.

## IV. *Of the Fruit and the Seed.*

§ 176. Fruit (*fructus*), in the scientific sense of the term, is the single pistil at the time of the perfect formation of the embryo (the maturity of the seed). The style and stigma, when they still remain, retain their names, but the germen acquires that of pericarp. In this sense, there are of course some plants which have no fruit, because they are not provided with a germen; these, therefore, must be described as naked seed-buds, and also naked seeds (*semina nuda*): to these belong the *Coniferæ*, *Cycadaceæ*, and *Loranthaceæ*. But there are also some particular plants in which the germen is easily destroyed, so that the seed-bud is developed in like manner without an envelope to the seed: these, in order to distinguish them from the former, are termed *semina denudata* (*Leontice* and *Peliosanthes theta*). The actual fruits may be divided, according to the analogy of the flower, into naked and covered (*fructus nudus et fructus tectus*), according as of the entire flower only the germen appears to exist (as in *Lilium*), or as this is surrounded by other floral parts (as in *Nicandra*). According as in a flower one or more pistils are developed, it is distinguished as simple fruit (*fructus simplex*, as in *Nigella*) from the multiple fruit (*fructus multiplex*, as in *Ranunculus*). Here, also, the arrangement of the fruit is to be distinguished just as the inflorescence was, and the same terminology may be retained (as fruit spike, fruit capitulum, fruit umbel, &c.); or simply, as Linnæus spoke of the flower of the *Compositæ*, so here as a compound fruit (*fructus compositus*), as in *Ananas*.

All that has been said respecting the nature of the individual germen, in reference to its origin, its composition, its interual divisions, &c., holds good of course for each several fruit, unless these conditions have been altered in the subsequent development and progress towards maturity; in which case such changes, but only such changes, must receive names.

The fruit may be defined in two ways, either as has been done in the paragraphs, or, as some botanists have attempted, as the whole individual flower at the time when the seed is ripe. It would be quite indifferent, fundamentally, for science, which definition were established, if only one actually were established: but the fact that not one single botanist has carried out the conception of the fruit consistently with his own definition has brought such confusion into the theory of the fruit, that,

increased still further by the want of knowledge of the germen, and the baseless gossip about explanations of striking phenomena, it has become a *crux et horror* to all who wish to devote themselves to the study of Botany.

It appears to me that the definition given in the paragraph, which agrees with that of most botanists, although, indeed, without therefore remaining true to itself, is the most to the purpose for the comprehension of the matter; besides, we should have no satisfactory word by which to denominate this most essential part of the flower, continuously developed up to the time when the seeds are ripe, if we applied the term fruit to the whole flower at the epoch of maturity. It is indeed self-evident, that botanists who have claims to scientific character may no longer content themselves with statements like "*pistillum unicum, stylus nullus, stigma simplex,*" and the like, but that a minute exposition of the rudimentary fruit, according to internal structure, number, and form of seed-buds, &c., is indispensable. Then, however, a quantity of phrases respecting the fruit become superfluous, which were formerly necessary, and are still partially retained from custom. It evidently follows that, putting out of the question the structural conditions, and the newly-formed embryo and endosperm, the construction of the fruit is exactly like that of the rudiment of it, and only requires especial notice when important modifications have occurred through actual abortion of seed-buds and entire cells.

Two very different points of view must be both established and accurately discriminated in the theory of the fruit, namely the scientific condition and the empirical denomination of the fruit. These two so wholly diverse respects have hitherto been completely confounded, and thence in reference to the first far too little, to the second far too much, has been done in the theory of the fruit. Here, also, this complication of aspects has been historically carried forward; and it is truly now time that we gradually strip off the still adhering egg-shells of newly-hatched science. It is indeed no long time since the more minute observation of the construction of the germen was first commenced; and so long as this existed merely in rough outlines, much that ought properly to have been previously mentioned necessarily came in as supplementary to the description of the fruit. That such patchwork does not go far, is, I think, sufficiently shown by our systems of fruits with their incompleteness, and yet at the same time with their arid waste of names and synonymes. It is clear, also, that no attempt to understand the fruit from the mere study of the ripe condition can succeed. The fruit is merely the final result of a series of developments of the whole plant, the last product of a great number of factors, and gives no conclusions about what has gone before, about the number and nature of the co-operating factors. Thus it has been attempted to deduce the number of parts forming the germen from the number of valves: it was only necessary to call to mind the *capsula circumscissa*, the *lomentum* and *legumen*, the loculicidal and septifragal dehiscence, to see that original composition and subsequent division stand in no necessary, but at most a very casual, connection. Pains have been taken to refer the separate layers of the pericarp to the layers of a leaf (carpel): but, disregarding the circumstance that leaves and pericarps do not universally exhibit layers, it is here most erroneously presupposed that every germen is composed of foliar organs, &c. Now if the construction of the germen has been perfectly understood, the gradual process of its development to fruit been comprehended,

the fruit requires no further explanation, it is self-evident; the product is always given by the factor, though the reverse never. All that relates to the form and composition of the fruit has, in a correct treatment of the science, been already given under the head of the germen and its developments; therefore the peculiarity of the fruit does not at all lie there, consequently none of this deserves special nomenclature. That an inferior germen cannot become a superior fruit is self-evident; and to distinguish the fruit again on this account is wholly superfluous. It is of more importance to state whether cells and seeds become abortive, or whether spurious septa have been formed during the growth of the fruit. On the other hand, the characteristic for the fruit and its essential peculiarity are its structural conditions, and hence these alone merit a peculiar nomenclature; for instance, the inferior capsule must be distinguished from the inferior berry, but not the inferior from the superior berry, since this latter character has already been given in the germen; and all that is additional in the fruit is the berry-like development of the parenchymatous layers of the pericarp.

Nowhere has purely diagrammatic comprehension been so prevalent as in the theory of the fruit; nowhere have botanists, starting from the language of common life, and merely multiplying the words, taken so little pains to define with scientific strictness; and hence nowhere does terminology so vacillate among all the definitions as in the fruit. One assumes 10, another 15, a third 20, and another 40 or 50 kinds of fruit; in short, the confusion is indescribable; and if, according to the best authorities, one explains to the scholar a *drupe* as a closed fruit, fleshy externally and woody within, a capsule as a dehiscent, dry fruit, he finds, in Reichenbach, for instance, not one single Labiate or Boragineous plant described, since this author ascribes to these four *drupes*, and the four drupes unite to form a capsule.

I find the best exposition of this complicated subject in Lindley (Introduction to Botany), who has at least sought to let in some light by logical arrangement and strict definitions. Yet it is clear that the existing wilderness of names, thrown together arbitrarily and under no principles, is too much for the most straightforward inclination. The only thing to be done is to throw away the whole mass, and begin the investigation over again.

We have almost as many systems of fruits as botanical writers. We owe the first thorough research into fruits and seeds to Gärtner (*De Fructibus et Seminibus Plantarum*, Stuttgart, 1788) and L. C. Richard (*Analyse du Fruit*, Paris, 1808), whose works will remain classic for all time. Subsequently to these, Mirbel, Dumortier, Desvaux, and others have given Systems which, without essentially improving anything, contain an innumerable quantity of new names, even for things long before known and named.

§ 177. Taking the foregoing for our standard, we have now to follow out particular points in the fruit. 1. We have to examine, as portions of the fruit, the pericarp, the spermophore, the funiculus, and the pulp; then again, the seed, and in this the episperm and the nucleus, and in this the embryo and the albumen.

2. We have further to take account of the remaining parts that stand in close relation to the fruit, from the bracts up to the parts of the flower: these are accessory organs.

3. Lastly, the various kinds of fruits are to be enumerated.

These matters, for the most part, require only to be generally mentioned and collected together here, since everything of importance relating to them has already been mentioned in the paragraphs (§ 160—175.).

### 1. *Of the individual Parts of the Fruit.*

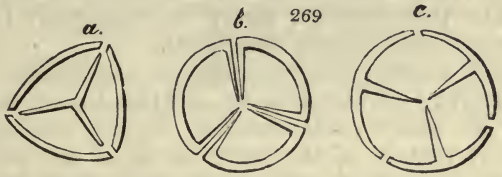
§ 178. The pericarp is the transformed germen: sometimes it is united with the other persistent parts of the pistil, style, and stigma. The latter are seldom of particular importance; and all that need now be said of them is that they have been retained up to this epoch (as in *Papaver*), or they have become more developed (as in *Pulsatilla*). The forms of the pericarp are exceedingly diversified, but admit of no general definition; they frequently exhibit hairs, prickles, protuberances, and membranous expansions (*alæ*), prominent ribs (*costæ* or *juga*), and pits in their interspaces (*valleculæ*), &c. The pericarp essentially determines the varied appearances of the fruit, by its diversity of structure. It has already been mentioned in what various manners the parenchyma of the germen is developed. In the simplest cases, we find in the mature pericarp only the epidermis of both surfaces, and between these an uniform layer of parenchyma, without vascular bundles (as in the lower *Araceæ*), or traversed by a few simple bundles. In other cases only the epidermis of the external surface is perceptible, whilst the entire parenchyma, with the epidermis of the inner surface, is succulent or fleshy (as in *Atropa*); or it may be, that under the epidermis of the outer surface some layers of cellular tissue are woody, whilst the underlying are fleshy; in both cases very frequently passing without determined boundary into the pulp.

In many other cases four layers are distinctly discernible, which have been already characterised; and since the time of DeCandolle (altogether misunderstanding L. C. Richard, the originator of the division) they have been named, counting from without inward, epicarp, mesocarp, (also sarcocarp, or flesh, *caro*); and the two inner undistinguished coats, the endocarp. Those varieties of structure in the fruit are most important which cause the peculiar solutions of the continuity in the fully mature condition. Hence we obtain two comprehensive classes of fruits, according as their construction causes a separation into individual parts or not. The latter may be termed the berry-like, and the former the capsular. The capsular are again divided into two groups, according as the pericarp either opens and suffers the seed to escape — capsules with their portions called valves, or separates into individual parts, which do no not again open, but firmly enclose the seed — splitting fruits (*schizocarps*), and their parts called mericarps. The berry-like fruits are also subdivided into three groups, according as the inner

layers are the more tough and solid, and the outer the more fleshy and juicy — stone berries (*drupes*); or the reverse — true berries (*baccæ*); or, lastly, all the layers appear thin and dry, or leathery (*achænia*). All these forms may, with the germen from which they arise, be superior or inferior, one- or many-celled or one- or many-seeded; which only require to be noticed when deviations in the structure of the germen have arisen through abortion, being otherwise self-evident.

*a.* The capsular fruits occur in the most diverse families. The mode of bursting (*dehiscence*) is especially to be observed. The simplest process is an apparent wholly irregular tearing open at any place (as in *Nicandra*): usually, however, the form of this dehiscence is very regular, even though it may be confined to a small part of the fruit (*pericarpium poro dehiscens*), as in *Papaver, Antirrhinum*, &c.

The solution of continuity is either vertical or horizontal: in the latter case, the upper part forms a kind of cover upon the under, and the capsule is termed circumscissile. In the first case, the pericarp, &c. falls away in more or fewer separate pieces, which are termed valves.* In many-celled fruits (*a*) the valves may




separate entirely from the persistent septa, as in *Cobæa scandens* (*dehiscentia septifraga*); or (*b*) the septa may split into two lamellæ, and each valve may bear one of these lamellæ on each of its margins (*dehiscentia septicida, valvulæ margine septiferæ*); or (*c*) the septa may remain undivided, adherent to the middle of the valves (*dehiscentia loculicida, valvulæ medio septiferæ*). If in any of these kinds of dehiscence a stalk-like mass of cellular tissue remains standing in the axis of the fruit, it is called the *columella.*

From what has been said, it is sufficiently evident that these solutions in the continuity are not at all dependant upon the original composition. Common Botany, however, assumes such a relation, and therefore applies to the line in the external circumference of the pericarp, where the edges of real or pretended carpels have become blended, the term of "dorsal suture," which is only half correct according to this very hypothesis, while the term "ventral suture" designates merely the line where the margins of one and the same carpel or similar part have become blended.

* Sometimes tough cords of cellular tissue, persistent between each two valves, connected in the stigma above (as in *Argemone*). I do not find that any special name has yet been made for these.

In the generality of capsular fruits, the above-mentioned four layers of the pericarp may be distinguished from each other; but they are usually very thin and membranous or leathery, or more rarely woody.

*b.* The schizocarps or splitting fruits are usually distinguished chiefly according to the direction in which the cleft occurs. This is either parallel with the axis of the fruit, or perpendicular to it, that is, the solution of continuity is either vertical or transverse. In both, the separate parts are usually only one-seeded. In the first case the separate parts are sometimes named *cocci* or *mericarps*, in the last case joints or articulations; and they are distinguished, according to the texture of their layers, as dry, coriaceous, and succulent. The first (the mericarps) are proper to the families *Rubiaceæ*, *Euphorbiaceæ*, *Labiatæ*, *Boraginaceæ*, *Geraniaceæ*, *Tropæolaceæ*, *Malvaceæ*, *Umbelliferæ*, &c. &c.; the last (the joints) to some of the *Leguminosæ* and *Cruciferæ*. In the first a *columella* is not uncommon.

*c.* The stone berries, characteristic of the *Amygdaleæ*, but also presented in other families, owe their peculiarity to the remarkable diversity in the structure of their layers, and indeed of the parenchyma layers, the inner of which are always hard, and often woody; whilst the outer are fleshy or coriaceous: both are developed in a greater thickness than usual.

*d.* The true berries, predominating in the families of *Grossulariaceæ*, *Passifloraceæ*, *Cucurbitaceæ*, and the *Araceæ*, and occurring occasionally in many other families, depend essentially on the fleshy or juicy texture of the inner layers of the pericarp: this condition often exists to the extent of a dissolution into single cells, tumid with fluid, whilst the external layers are solid, and sometimes even woody (as in *Lagenaria*).

*e.* The achænia, with always thin dry layers, not usually distinguishable, characterise the families of the Grasses, *Cyperaceæ*, *Cupuliferæ*, *Compositæ*, and *Dipsaceæ*, predominate in the *Dryadeæ* and *Ranunculaceæ*, and occur singly in other cases. They are one-celled and one-seeded, generally originally, but sometimes (as in the *Cupuliferæ*) through abortion of cells and seed-buds.

I really believe that the five expressions here given for the nomenclature of the forms of fruits are perfectly sufficient for the present, if botanists would once begin to seek science in profound knowledge of the vegetable organism, and not in miserable scholastic trifling with the manufacture of Greek and Latin, classic, or even crass,— barbaric words. In the enumeration of the particular words now in use, below, I shall have plenty of opportunity for criticism. Here I will merely remark, that the very same botanists who have set up a splendid general Fruit system, often lay aside all these fine words in the special working out of plants, and come off exceedingly well with a very few terms, which is in fact a confession that in the general treatment of the theory of the fruit they have been playing an unaccountably frivolous game with the reader or student. In any case, the manner in which the French in particular have increased nomenclature, is contrary to all laws of a sound termi-

nology. Many as there are who praise or condemn Linnæus, call him great or unintelligent, of all these not one has understood him, not one seen what he really attempted and how he attained it. It was a war against the nomenclature, heaping itself up with nothing but substantive words, which he began and happily carried through, by which means he, as with a magic touch, opened a thousand entrances into science previously impassable. A second Linnæus is indeed very desirable, and will be made most necessary by those very people who especially pride themselves on being able to look down upon him. The wiser do indeed admire the artifice of Linnæus, but continue boldly to make names daily, because they are not in a condition to abstract the universal principle from the isolated cases of the application. Here, as everywhere, it is requisite, in the first place, to discover inductively the various genera of the natural ideas, and these alone are to be named with substantives, their species to be separated by the addition of adjectives. This assists a rational investigation of nature, and a rational terminology. In all this manufacture of words, we have in fact learned nothing at all about the fruits themselves; Botanists who have spread themselves out in every new book with twenty or thirty new Greek names, are often so ignorant of the *proper* object of their research, that they call the epidermis of the fruit of the *Labiatæ* a seed-membrane, derive the cross septum of *Punica* from the disc, &c.; and, in a word, manifest everywhere that the study of the Greek language has unfortunately left them no time to examine deeply into plants. Consequently we possess so few accurate investigations of the fruit, that it will be long before our knowledge of it will be even in the least endurable; and therefore we must so much the more content ourselves with the smallest number of names, because a man must know a thing before he names it scientifically.

§ 179. The nature of the spermophore has been already discussed at length, and but little remains now to be added. In the first place it is to be remarked, that in the dehiscence of the fruit, portions of cellular tissue are separated from the valves or septa, to which the seeds remain suspended, and which have, indeed, been termed spermophores. Here, again, holds good what has been said of these separations in general, that sometimes actually independent organs become solved from their union with others (as in *Cruciferæ*), and sometimes merely pieces of independent organs become detached (as in the *Asclepiadaceæ*).

It has been already observed with respect to the pulp, that on the one hand it passes into the loose cellular tissue of the pericarp in the true berries (as in *Solanum*), and on the other into the subsequent products of the funiculus; namely, into the aril in its widest sense (in *Arum*), and probably into the true aril (in *Ribes?*).

The funiculus exhibits manifold varieties, which have already been explained, such as hairs, warty expansions among the seeds, membranous, continuous, or lobed envelopes of the seed (*arils*), and so forth. The hairs of the funiculus form one kind of coma; the other is a development of the episperm at various places, at the micropyle or the chalaza. The wart-like expansions on the seed are termed *strophiola* or *caruncula*, but have under these names been mixed up

with very different things, e. g. processes from the micropyle. The formations of the aril are very various, and differ especially in regard to colour, texture, and cell-contents.

All the conditions here mentioned have already been explained in previous sections; here it suffices to notice them again in connection.

§ 180. The most important part of the whole fruit, as regards the economy of the plant, is the seed (*semen*), because it encloses the embryo, which is destined to perpetuate the species. The seed may be quite free, without a pericarp, as in the *Cycadaceæ, Coniferæ,* and *Loranthaceæ.* Here the seed assumes quite the appearance of a fruit; for instance, of a winged achænium in the *Abietineæ,* of a berry in *Viscum,* and of a drupe in *Cycas,* &c.

In the seed two parts are to be distinguished, the episperm and the nucleus; the nucleus is either formed solely by the embryo, or by that and the albumen. Then, again, the regions of the seed are distinguished as the base, the part by which it is attached, and the apex, the free point opposite to the former. The position of the seed in the fruit is determined according to the relations of these parts. The fruit is supposed to be erect, its base downward, and the seed, of which the point stands higher than the base, is termed *erect,* when it is attached at the bottom of the cavity of the fruit; *ascending,* when it arises from the lateral wall. Seeds of which the apex is lower than the base are termed *suspended* or *pendulous;* if the apex and the base lie on the same level, the seeds are termed *horizontal,* or sometimes indeterminate (*vaga*). When the line from the base of the seed to the apex forms not the longest but the shortest diameter of the seed, it is styled *peltate,* or *medio affixa.* In the loose seed, that surface by which it was connected with the funiculus is termed the *hilum* or *umbilicus.*

All these terms would be rendered quite superfluous by the adoption of a better method, since the position of the seed follows from the position of the seed-bud; but as the generality of our present books do not enter into the structure of the seed-buds in the description of families, much less in the characterisation of particular species, the preceding remarks were required for the comprehension of our existing literature.

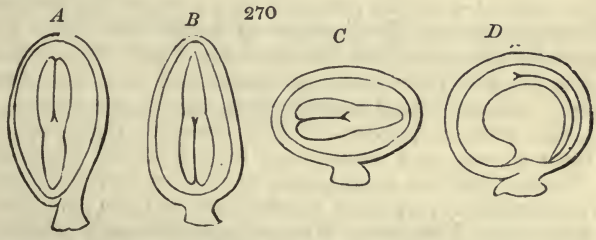
The episperm, as explained above, allows no general reference to the coats of the seed-bud, and, therefore, we can only speak generally of one episperm, and we must characterise the individual cell-layers (*strata*) more minutely when the history of the development of the particular species, genus, or family is still unknown. The epidermis of the seed may be almost universally distinguished from the episperm with advantage. On its surface are described hairs (issuing from the micropyle in a tuft), as *coma,* papillæ, prickles, ribs, wings, &c., and the regions of the raphe, of the chalaza, and of the micropyle.

The old school doctrine, here quite wrong, says that the coat of the seed consists of two membranes, the proper coat of the seed (*testa, lorica,*

*spermodermis, tunica externa*), and the internal membrane (*membrana interna, tunica interna, endopleura, tegmen*). The first of these is sometimes the outer, sometimes the inner integument, sometimes only the epidermis of the one or the other; the second is sometimes the outer integument excluding the epidermis, sometimes the inner, and sometimes the nuclear membrane; and if the epidermis of the outer nuclear membrane is developed succulent, DeCandolle has yet a third term, namely, the sarcoderm; or sometimes the outer, and sometimes the inner coat of the seed may not exist. There have naturally been endless contests whether the vessels run in the outer or inner seed-coats, and more of the like confusions, which necessarily must arise from the unmethodical manner of treating the subject. It has already been observed, that the separate layers of cells of the episperm can only be referred to the integuments of the seed-bud by tracing the development in the individual cases; when this has not been done, we must be content to describe such layers as are distinguishable, without further talk about their unknown origin.

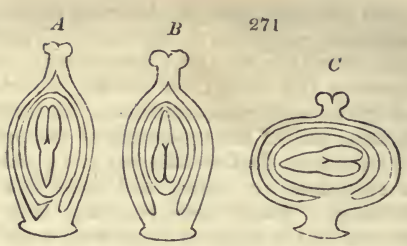
The *albumen* is either endosperm or perisperm, and its texture may be fleshy, horny, or otherwise varied; if marbled by brown, half-decayed lobes of the episperm, penetrating into its substance, it is said to be *ruminated;* its contents are mealy, oily, &c.

The embryo is mono-, di-, or polycotyledonous, erect, curved, spiral, &c.; enclosed in albumen, lying at the apex of this (usually falsely called the base), or encircling the albumen (*embryo peripheric us, albumen centrale*), &c. Its position in reference to the seed is invariably so determined that the point of the radicle is directed to the micropyle. Through this law the whole of the former temporary terminology has become quite useless, but it is still retained; it is double: —




1. According to L. C. Richard, the seed, supposed erect upon its base, has, *A*, an *embryo orthotropus* or *erectus*, if the root is directed towards the base; *B*, an *embryo antitropus* or *inversus*, if it is towards the apex; *C*, an *embryo heterotropus* or *vagus*, when it has a direction intermediate between the two; and *D*, an *embryo amphitropus*, when the embryo lies curved into a circle in the seed.

2. The terminology of older date, still much in use, refers the terms to the unchanged position of the seed in the fruit, supposed to be upright, and it speaks of, *A*, *radicula infera*, when it is directed to the base of the pericarp; *B*, *radicula supera*, when it is directed to the apex of the same, and, *C*, *radicula vaga*, when it is directed




to the side walls. Finally, the forms of the embryo itself have been sufficiently explained in the preceding pages.

### 2. *Of the accessory Organs of the Fruit.*

§ 181. The parts of the flower external to the germen persist in part until the maturation of the seed, often undergoing many changes, especially as regards their texture, which not infrequently becomes fleshy; hence they sometimes assume the appearance of fruit (spurious fruit). As examples of this may here be offered the peduncle (in *Ficus*), the pedicel (in *Hovenia dulcis*), the bracts (in *Ananassa*), the perianth (in *Morus*), the calyx (in *Cucubalus baccifer*), the corolla (in *Mirabilis*), the disc (in *Rosa*), the receptacle (in *Fragaria*).

In a similar condition to the close connection in which calyx, corolla, &c., stand to the other organs of the flower, the organs of the nearer (calyx, corolla, perianth, disc, receptacle, &c.) or more distant (pedicel, epicalyx, bracteoles, bracts, peduncle, &c.) parts of the flower persisting or undergoing further development up to the time when the fruit is mature, come into nearer relation with the fruit. The different points of view under which the forms are conditioned here, have been already explained. The structural conditions are also important here, since frequently the most heterogeneous parts undergo transformations which cause them to assume a resemblance to any of the forms of the true fruit. We even find the development of the four layers occurring in the pericarp, expressed in a similar manner here in these parts, for instance, in the perianth of *Elæagnus*. Where simply the calyx persists, growing in its green condition, and then becoming membranous or thinly woody, no regard has been paid to it, and it is simply called *fructus calyce textus*, or the flower merely is said to have *calyx persistens;* but where a different alteration of the texture has taken place, and these accessory parts specially enclose the true fruit, a peculiar form of fruit has been made of it, and a technical term soon found; and thus, with double inconsistency, the organs become fleshy are made kinds of fruit (the peduncle of *Ficus*), while those altered in a different way (the peduncle of *Urtica*) are not: then again, some of them changed into a fleshy condition are described as what they really are, e. g., the fleshy peduncle of *Anacardium*, which no one has proposed to make a special kind of fruit. The whole of the terminology arisen out of these considerations is superfluous, since the further development ought to be always indicated in the de-

scription of the flower to make the fruit comprehensible; and if we say *calyx persistens*, we may just as well say, for instance, in *Morus*, *perianthium demum carnosum* . . . . . *fructus achænium*, by which the matter is more clearly and simply characterised than by a new, wholly superfluous, technical word "*sorosis*," which can certainly only be of use in this one genus; for in the mass of vain distinctions which have received special names, it is an inconsistency, ridiculous beyond all description, to characterise by one term the fruit of *Ananas*, an inferior, thin-celled berry; of *Morus*, a two-celled (?), by abortion one-celled, thin-walled achænium; and of *Artocarpus*, an originally one-celled, membranous pouch.

For those who define the fruit as the total flower at the epoch when the seed is mature, the matter is equally bad; what I blame here is merely the ignorance and the inconsistency arising from want of principles; since, if the fruits of *Morus*, *Ananassa*, and *Artocarpus* are brought together as a special kind on account of the *perianthium demum carnosum*, the fruits of *Hyoscyamus*, *Nicandra*, *Physalis*, and *Atropa* must also be jumbled into one kind on account of the *calyx persistens demum lignoso-membranaceus*, which no one would agree to do.

### 3. *Enumeration of the various Forms of Fruit.*

### § 182.

I. Seed naked (*semen nudum*).

*A.* Seed solitary.

1. *Bacca**, seed inferior, e. g. *Viscum*.
2. *Sphalerocarpium*, seed with a fleshy aril, e. g. *Taxus*.

*B.* Fructifications.

3. *Strobilus*, spikes with woody spermophores, e. g. *Pinus*.
4. *Galbulus*, Capitula with confluent fleshy bracts, e. g. *Juniperus*.

II. Simple fruits (*fructus simplex*).

*A.* Capsule (*capsula*).

† Superior.

5. *Capsula circumscissa*.
6. *Utriculus* Gärtner, No. 5. one-celled, originating from a carpel, few-seeded, e. g. *Chenopodium*.
7. *Pyxidium*, No. 5. one- or many-celled, formed of several carpels, many-seeded, e. g. *Hyoscyamus*.
8. *Folliculus*, one-celled, many-celled, one-valved. Seeds on the two margins of the valve, e. g. *Pæonia*.
9. *Conceptacula*, two disunited *folliculi* with one separating spermophore, e. g. *Asclepias*.
10. *Legumen*, one-celled, 1—, many-seeded, two-valved. Seeds on the two borders of one fissure, e. g. *Pisum*.

* The names spread out in the (*Italic*) type are in tolerably universal use.

11. *Siliqua*, two-celled, two-valved, separating from the persistent spermophore, forming a septum (*replum*), e. g. *Matthiola.*
12. *Silicula*, a very short *siliqua*, e. g. *Thlapsi.*
13. *Ceratium*, a *siliqua* in some *Fumariaceæ* and *Papaveraceæ.*
14. *Rhegma*, elastically two-valved (?) dehiscing from a *columella*, e. g. *Euphorbia.*
15. *Capsula*, one- or many-celled, many-seeded, dehiscing by valves or pores, *Primula, Antirrhinum.*

†† Inferior.

16. *Diplotegia* Desvaux, inferior capsule, dehiscing by pores, e. g. *Campanula.*

*B.* Splitting fruits (*Schizocarpium*).

17. *Cremocarpium* (?), in *Umbelliferæ, Rubiaceæ.*
    *a. Mericarpia*, the separate parts of the *schizocarpium.*
18. *Carcerulus*, in *Tropæolaceæ, Malvaceæ.*
19. *Achænium*, in *Boragineæ, Labiatæ.*

*C.* Stone fruits (*drupa*).

20. *Drupa*, originally one-celled, 1— 2-seeded, the *mesocarpium* fleshy, the *endocarpium* woody, e. g. *Amygdalus.*
21. *Tryma*, (imagined to be) one-celled by suppression in *Juglans.*

*D.* Berry (*bacca*).

22. *Bacca*, many-celled, inferior, e. g. *Ribes.*
23. *Nuculanium*, many-celled, superior, e. g. *Vitis.*
24. *Pepo*, one-celled, inferior, e. g. *Pepo.*
25. *Hesperidium*, coriaceous portion strictly separated from the pulp, e. g. *Citrus.*
26. *Amphisarca*, woody toward the exterior, e. g. *Crescentia.*

*E.* Closed fruit (*achænium*).

27. *Achænium* (*auctorum*), *cypsela* (Lindley), one-celled, one-seeded, not blended with the seed, e. g. *Compositæ.*
28. *Glans*, through abortion one-celled, one-seeded, e. g. *Corylus.*
29. *Caryopsis*, one-celled, one-seeded, (imagined to be) blended with the seed, e. g. the Grasses.
30. *Samara*, two-celled, winged, e. g. *Acer.*
31. *Carcerulus*, many-celled, not winged, e. g. *Tilia.*

III. Multiple fruits (*fructus multiplex*).

*A.* Several achænia.

32. *Etærio*, if wholly free, e. g. *Ranunculus.*
33. *Syncarpium*, if connected, e. g. *Magnolia.*

*B.* Several berries.

34. *Etærio*, connected, e. g. *Rubus.*

IV. Fructifications (*fructus compositus*).

*A.* Capitula with a flat or cup-shaped, fleshy peduncle.

35. *Syconus*, e. g. *Ficus, Dorstenia.*

*B.* Spikes with fleshy bracts and perianths.

36. *Sorosis*, e. g. *Ananassa, Morus.*

*C. a.* Spikes with woody bracts.
37. *Strobilus*, e. g. *Betula.*
*b.* Spikes with woody bracts and perianths.
38. *Strobilus*, e. g. *Casuarina.*

V. Spurious fruits (*fructus spurius*).
39. *Cynarhodon*, free, one-seeded achænia, surrounded by a fleshy disc, e. g. *Rosa.*
40. *Pomum*, many-seeded achænia in one circle, blended with the fleshy disc, e. g. *Malus.*
41. *Balausta*, many-seeded achænia in two circles, blended with the fleshy disc, e. g. *Punica.*
42. *Diclesium*, achænia enclosed in a hardened perianth or corolla, e. g. *Spinacia, Mirabilis.*
43. *Sphalerocarpium*, achænia enclosed in a drupaceous perianth, e. g. *Hippophäe.*

I did not intend to give a complete enumeration in the paragraphs of all the names of fruits hitherto proposed: many of them would be too much honoured by being named merely to be thrown away. I have here only retained those most in use, and introduced by at least one botanist of consideration (besides the author); in the first place, in order to show how they range themselves under those which appear to me fully sufficient for the present, partly to make the beginner at least acquainted with the generally accepted words, and partly to allow of connecting with them some critical observations on the whole theory of the forms of fruits. I will first endeavour to exhibit, in a brief sketch, how the matter has historically developed itself, since only in this way can the total insufficiency of this theory be in some measure comprehended.

Besides the expressions of common life, which defined useful fruits partly according to their outward, readily perceived differences, partly according to the diversity of the plants called by different names, of which the itself yet unscientific Science took up some, certain other names were very early made, necessarily requisite to denominate things for which common language naturally had no expressions, because they did not immediately serve any of the purposes of life. Thus little juicy fruits were, without distinction, called berries, but *malus* and *pyrus* were distinguished as apple and pear: apple, as a *kind* of fruit, has never been the language of common life. Expressions like *acinus, pilula, folliculus*, &c., which occur in authors anterior to Linnæus, were never vernacular words. Up to his time any scientific treatment of the general part of Botany was out of the question; the forms were conceived diagrammatically, and described somewhat in the same manner. Linnæus first gave definitions, and an arrangement deduced from a general survey of the conditions known to him. He distinguished the fruit (*fructus*) from the seed (*semen*), and combined under the latter head, also, all one-seeded splitting and closed fruits (schizocarps and achænia, &c.). The former he divided according to its composition from different parts and their structural condition, in which he gave in far too much to the common custom of language, and thus obtained sections of very unequal value. He had no correct principle of division, and, in his imperfect knowledge of the development of the fruit, he could by no means find such. On his foundations others afterwards built, and untenably, since the only

sure ground, accurate knowledge of the unimpregnated germen, was professed by no botanist. The want of a subdivision into classes, orders, genera, and species, deduced from safe inductions, was continually more felt. Linnæus had placed his forms of fruit side by side as homologous members: the enlarged circuit of knowlege of materials rendered that enumeration of forms insufficient; and as new peculiar phenomena occurred, new forms with new names were added, without further trouble about the groundwork. This reproach especially applies to that profound observer of individual things, Gärtner, the very superficial Willdenow, and Link, who always judges from solitary, accidental ideas. In this, as so frequently in his casual notions, Link, of course, has a perfectly correct idea, but usually he wants the scientific earnestness to work it thoroughly out. He says, a very mistaken path has been taken in making so many new words for solitary distinctions of fruit, since individual different organs may indeed require especial words, but not their modifications. Nevertheless he receives the whole of the old nomenclature, which, in reference to the number of actual differences, is partly made up of terms for very inessential modifications, and he adds another new word to it. In the second edition of his Philosophia Botanica (vol. ii. p. 253.), he says, Linnæus, Gärtner, and Richard had given so many good descriptions of fruits, with their terminology, that he would refrain from all new technical terms, and only add *amphispermium* as a collective term for *achænium* and *caryopsis*. Nevertheless he made a wholly new definition for *achænium*, called the old caryopsis *seminium*, formed again two species of the new *caryopsis*, according to characters actually non-existent, and called one *carpelletum*. Besides these, he speaks only of *capsula*, *pomum*, *legumen*: nothing is said of all the rest of the kinds of fruit; and it is not stated at all how the introduced expressions are to be applied to *siliqua*, *drupa*, *bacca*, *hesperidium*, &c. L. C. Richard first (Analyse du Fruit, Paris, 1808), and subsequently DeCandolle (Organographie Végétale, Paris, 1827), making use of the knowledge of the structure of the germen by that time collected, sought, with somewhat more philosophic spirit, to give a new basis to the matter. But they remained in the bonds of conventionality, and so allowed a number of subordinate conditions to stand as homologous members beside main divisions. L. C. Richard first distinguished the *four* layers, mentioned above, in the pericarp, namely, the *epicarpium* and *endocarpium*, as external and internal epidermis, and the *mesocarpium* as parenchyma between the two: of this latter, he added, one layer is often separated, which forms the stone in the drupes, &c. He therefore distinguished this layer strictly from the endocarpium, because his distinction depended on minute observation. DeCandolle, however, confused the whole matter again by introducing an imaginary theory, tracing those three layers to the layers of a leaf, to which, from imperfect knowledge of its structure, he ascribed three, and only three, layers. Thus he made the endocarpium the third layer, counting inwards, and mixed it up with Richard's endocarpium, wholly overlooking the woody layer of Richard's mesocarpium. Thus a pretended theory, without observation, turned an excellent observation into a mass of confusion. DeCandolle did the same with Richard's terminology for the direction of the embryo, which he wholly misunderstood, and consequently ascribed a superior radicle to the embryo of *Ceratophyllum*, nearly a quarter of an inch long, truly easy enough to observe. DeCandolle, indeed, started from the perfectly correct axiom, that the

fruit must be explained from the construction of the germen, but in the application all went awry again, because he did not understand the structure of the germen itself. Neither he nor any of his followers had philosophic training enough to abstract the general law from the isolated concrete cases, and yet it lay near enough when it was seen that the fruit could not be understood without a knowledge of its development, that consequently this must apply also to the germen. But a great obstacle met them there: it would have required microscopic research, and that was too inconvenient. By the hasty examination of a few monstrosities, and the spinning of a pretty fiction, the goal was sooner arrived at: thus arose the prejudice that every germen must be composed of foliar organs, and thereby every correct treatment of the theory was cut short.

More recently Mirbel, Desvaux, and Dumortier have given great Fruit Systems, but fortunately without their most barbarous words finding an entrance into science. Lindley alone has taken the pains to establish some of them, partly with new definitions. But he also, in their practical application, for instance, in his Natural System, is reasonable enough to leave the whole really quite insufferable wilderness of names out of the question. A few expressions have again been brought into use recently by Endlicher. On the whole, however, in most of the best authors, we find no terms besides those printed in spread italics in the paragraphs. Reviewing the treasure we have acquired, and the application we make of it, it must be confessed that we are still the slaves of the language of common life, since scarcely one technical term is established except those taken from it. All the rest rock about without principle or consistency. The capsules, so very diverse in the number of their cells and seeds, in the construction of the septa, mode of attachment of the seeds, superior or inferior, with the most varied kind of dehiscence, we call capsules; but, faithful to common language, we distinguish them only as pod, husk, or shell from the most unimportant characters. For the remarkable structure of *Hovenia dulcis* and *Anacardium* we have no special term; but the Fig has a proper title, because it comes into the domain of the table. *Utriculus, achænium, caryopsis,* are distinguished by the most trifling characteristics; but the Palms have berries and drupes, and under these are united the Cocoa-nut, the Date, and the fruit of *Sagus* and *Lepidocarya.* Every botanist, even only a beginner, must be terrified at the slightest reflection on the unbearable terminology which must arise if men continue to name such distinctions as those between *utriculus, achænium,* and *caryopsis,* with special names. The above arrangement of technical terms affords sufficient opportunity for such remarks. What totally different things are denominated by the expression *strobilus,* for instance! Of the superior capsule, often from the most trifling distinctions, nine kinds; of the inferior, only one, and that has not yet received a special name from any one. *Folliculus* and *legumen* are only distinguished through the dehiscence of the dorsal suture in the latter; but the most essential distinction, whether a capsule generally tears regularly or wholly irregularly, as, for instance, in *Nicandra,* is altogether disregarded. A completely inferior fruit (in *Compositæ*) is named *achænium,* as well as a quarter of a fruit, formed of half a carpel, in a superior fruit (in *Boraginaceæ*). *Drupa* and *tryma* are distinguished solely through the ignorance of the author of the latter name; since in *Juglans* there is never even an indication of a second cell, which is wholly impossible with the single basilar seed-bud. *Nuculanium* is a word merely intro-

duced through a misconception. L. C. Richard called a *drupa* a *nuculanium*, which contained several stones, each containing one seed, because he thought that in berries with a hard seed there must necessarily be an envelope of the pericarp over the seed. But how many study L. C. Richard? Apparently, not even his son, who applies to the expression *nuculanium* the meaning of an inferior berry. L. C. Richard, as the examples given by him show, never thought about superior and inferior. Since the name was once there, A. Richard applied it to the superior, Lindley to the inferior berry, while otherwise very few superior and inferior fruits are distinguished. This may suffice, not to complete the criticism of the present theory of the fruit, but to show by some examples how just the objection is which would reject the whole. See also the accordant views of H. von Mohl (Botanische Zeitung, 1843, p. 3.)

Next to the store of these technical terms we have to consider their application. With the language of common life, which establishes distinctions of the very slightest scientific importance, botanists have gradually introduced certain words, as above named. In the application of Fig and Apple no mistake can of course easily be made, since the words have been in daily use since infancy; but how stands it with the rest, which properly belong to science? A selection of examples, very hastily selected, may suffice to show. The Grasses have, according to Endlicher and others, a *caryopsis;* Link, a *seminium;* Reichenbach, a *nucula:* the *Cyperaceæ*, according to Koch, a *nux;* Endlicher, a *caryopsis;* Kunth, an *achenium;* Reichenbach, a *nucula;* Link, a *carpelletum:* the *Labiatæ* and *Boraginaceæ*, according to Endlicher and others, *achenia;* Lindley, *nuces;* Reichenbach, *capsulæ;* the *Labiatæ*, according to Link, a *carpelletum;* the *Boraginaceæ*, according to Link, a *caryopsis:* the *Ranunculaceæ*, according to Link, a *carpelletum;* Koch, a *carpellum nucamentaceum;* Lindley, a *nux* or *caryopsis;* Endlicher, *achenia;* Reichenbach, *carpidia:* the *Umbelliferæ*, according to Koch and others, 2 *mericarpia;* Link, 2 *achenia;* Lindley, 2 *carpella;* Endlicher, 2 *carpidia;* Reichenbach, 2 *drupæ*. I have thought this fully sufficient to place glaringly enough the wretched condition in which our science is sunk before the eyes of the blindest of its worshippers. That here the vanity of the individual who has an opinion of his own, on any point whatsoever, no matter how subordinate, will so much the less make a sacrifice to the general good the more he is conscious in himself of having neither inclination nor skill to do anything really great in science, — that this curse, which is especially the visitation of botanists, may have a share in this anarchy I will not wholly deny; but since most of the men named stand at the head of the science, one may confidently conclude from such facts, that the rotten places are to be sought not in the individual, but in the distorted position which the whole science has assumed through manifold historical conditions, so that of course the individual, proceeding on such a path as supporter of the same *bona fide*, is not to be blamed.

I think that for the present, with the correct naming of the naked seeds and the compound fruits, and the correct distinction and characterisation of the spurious fruits, the five kinds of fruit I have given (A—E) will fully suffice to name the little that remains to be named, if a better and more profound method than we have hitherto had, allow the minute description of the germen and the statement of the peculiarities in its mode of development to precede. Most of the conditions

of the fruit, which have hitherto been named with different technica terms, belong necessarily to the description of the germen, and it is therefore a tedious waste of time to repeat them again in the fruit when no alterations have taken place. What are new and peculiar in the fruit, are the structural conditions, and the diversity of dehiscence depending on those. The former are amply characterised by only four terms; the latter have hitherto been correctly named, for the greatest and most essential part, with adjective terms; and therefore the few cases in which authors have inconsistently enough amused themselves in doing otherwise, the substantive in question may be at once expunged.

In conclusion to this whole morphological investigation, I will once more express my *Ceterum censeo:* There can be no Science of Botany without the Study of Development.

# FOURTH BOOK.

## ORGANOLOGY.

§ 183. ORGANOLOGY embraces the doctrine of the life of the whole plant, and of its particular organs. Life is the activity of those powers inherent in the matter constituting the form of the plant, and which present themselves as the special life of the plant.

Organology is less understood than any other part of botanical science; a large field of unexplained phenomena remains, which are comprehended as a whole, because we are too ignorant to separate the individual powers from their combinations, or again to reconstruct them. This unknown region we designate by the term life, or organic life, and its complex cause we term vital power or principle. But this is only a negative term, and can never be assumed as a ground on which to found future explanations in our science.

The life of plants is designated, to distinguish it from that of (the higher) animals, as vegetable or vegetative life. This distinction is in the highest degree vague; it rests chiefly upon the growth and development of forms, and upon the chemical processes of the plant. In these last a certain periodicity is frequently presented to us. The chemical processes proceed very quickly (as in the growth of plants during summer, or the rainy seasons of the tropics), or very slowly, apparently almost standing still (as in the spore and embryo in the winter, or in the dry seasons of the tropics).

I have previously explained what I understand by life : I must here again refer to it.

In all times a distinction has been made between animal and vegetable life, but, owing to the paucity of our knowledge, it has hitherto been impossible to draw a direct boundary line between the two. The change of inorganic matter into organic matter, united with the formation and development of new forms, and particularly of new elementary parts, is meant by most writers when they speak of vegetation, vegetable life, &c. That the life of plants embraces much more than these two functions is very evident, but the remaining processes are not so strikingly apparent, and certainly not so evidently dependant upon external influences and physical powers as the two first. We are accustomed to consider plants as lower and less self-dependant organisms than animals, and we attach especial importance to those indications which point to their dependance on physical phenomena (Erdleben *). As the formation of new structures

* Erdleben is earth-life. Amongst the German writers it is not uncommon to call the sum of physical phenomena presented by the earth a lower kind of life. In a posthumous work by S. T. Coleridge, entitled the "Idea of Life," the same view is adopted.—TRANSLATOR.

is closely connected with the presence of the matter of which they consist, so must they be quite dependant upon the chemical processes which furnish this matter. These chemical processes are subject to all the different changes or modifications of acceleration, retardation, &c., which are occasioned by variations of temperature, light, pressure of air, and electric tension. In this manner the life of plants is connected through these chemical processes with planetary phenomena, and affected, both mediately and immediately, by planetary changes. Upon these changes depend all the periodical phenomena in the life of plants, the greater part of which are entirely unknown to us, whilst even the more easily comprehended phenomena have been only superficially observed, and this in their relations rather than in their essential forms.

In the following paragraphs I shall briefly allude to this part of the subject.

This periodicity displays itself in a double manner: —

1. In certain parts of the plants (as the spore, the pollen-grain, and the embryo), the chemical processes appear almost to stand still, so long as no stimulating external cause excites them. There is, however, by no means an entire cessation of the germinating power of the seed, or it must lie in eternal sleep. This process is constantly carried forward, though sometimes almost imperceptibly. It goes on in different plants at different periods, according as external influences awaken anew the chemical processes which give to it other directions; again its activity is extinguished, again to be renewed by external agents, and the result is what we call life. These outward influences only serve to disturb and stimulate the elements of matter, and thus make evident the universal life of nature.

2. The chemical processes of the entire plant are influenced with great precision by the relations existing between them and the physical changes of the earth and its regions, also the alternation of winter and summer, day and night, and the variation of weather produced by them.

In relation to the first point, we may consider the earth as divided into four regions: 1. The equatorial region, where vegetation never appears to be interrupted, because the heat and moisture are comparatively equalised throughout the year; 2. The next adjoining region, where the periodical deficiency of moisture retards the chemical process; 3. The belt lying next, which is of considerable width, and in which the periodical decrease of warmth has the same effect; and 4. The polar regions, where the small measure, both of warmth and of moisture, almost precludes the possibility of vegetation.

Of the second, the summer sleep of plants, Martius, in his Flora Brasiliensis, has given an interesting illustration. We are ourselves, in our latitudes, annual witnesses of the winter sleep of plants, as we observe it at least in the appearances to which it gives rise, though as yet we little understand it. But in this sleep there is only decrease of activity in the chemical processes — no actual cessation of them. For though the coldness of the temperature may have become such as to cause almost a suspension of these chemical processes, yet they are again stimulated by the action of atmospheric causes; although, for a short time, the matter of the plant may remain in the same circumstances, the gradual return of the external influences will cause the chemical processes to resume their vigour, and vegetation proceeds in its old course: this may be seen in the careful thawing of frozen parts.

The alternation of night and day exercises a similar influence, though

in a less striking degree. We are at present only acquainted with some of the results of this alternation, of which we shall speak under the phenomena of motion.

The influence exerted by the changes of weather is less understood. Those tribes of plants which are most especially dependant upon atmospheric influence, as Mosses and Lichens, exhibit very evidently the action of moisture. It is also well known, that after a tempest an evident revivification occurs in the vegetable kingdom. But these observations must remain superficial and fragmentary, as it is only recently that the facts of meteorology have assumed a scientific form. On this part of our subject only general remarks could be made, as all special scientific observations are deficient. For example, what changes take place in the contents of the vegetable cells, and what chemical processes pass in them with the approach of winter, how far those processes are affected by warmth, light, and electricity, are all problems which must be solved before we shall have gained even a sure foundation on which to work. The field of investigation lies open before us, but at present it has found but few profound or original cultivators.

§ 184. Organology embraces the phenomena of life in the whole plant (general organology), and in the individual parts as especial organs (special organology). The life of the entire plant is the result of life in its individual cells; we shall therefore gain no insight into our subject, and no possibility of explaining it, so long as we are unable to trace back the general results of vitality to their origin in the individual cells. Hitherto, in the absence of a right method of investigation, little has been done. The consideration of this part of organology must, therefore, consist principally in stating correctly the problems involved and the mode of solving them. The same, also, with respect to that part of the science which has its foundation in morphology. There it must be discovered what morphologically-similar organs the plant possesses; here it must be considered how far morphologically-similar organs present also similar phases of the universal life of the cell, and how far they may thereby be converted into physiologically-similar organs.

Both parts of the subject must be pursued in plants arranged in morphological groups; but such investigation cannot at present be carried on, for all we should get would be a loose mass of superfluous and valueless paragraphs, for with respect to the generality of plants, and parts of plants, observations are wanting. I shall arrange the study of this subject in the following manner: — *A.* General organology. 1. General phenomena in the life of the entire plant: its life, germination, growth, nutrition, reproduction, death. 2. Special phenomena: the development of warmth and of light, movements. *B.* Special organology. A. Organs of vegetation: *a,* naked spores; *b,* covered spores. B. Organs of reproduction: *a,* Cryptogamia; *b,* Phanerogamia.

If we consider the attempts that have hitherto been made to subject the life of plants to scientific observation, we shall find that all those who have

conducted them have brought to their works groundless prejudices, and, following the old beaten tract, have not even paused to inquire whether or not it were right, and whether or not their prejudices were just; and they have even taken these latter as leading maxims to form the basis of all their investigations. I have already discussed the fanciful analogy between the physiology of animals and of plants. In consequence of the use of this absurd analogy, almost all the works which have hitherto appeared on vegetable physiology are perfectly worthless, for in no instance have they adopted the only true fundamental position, namely, the essential peculiarity of vegetable life; nay, the larger number of writers have not even given a comprehensive view of the facts already known, as such would have destroyed their assumed principles.

Each branch of natural science, if it would lay claim to such name, must have its own peculiar independent principle of development, which must be drawn from its own data, and *only* thence. It is not until considerable advance has been made towards perfection that it is safe to begin to inquire whether analogies exist between itself and some other branch of natural science, and, if so, what they are. The manner in which science is usually pursued is not following it out gradually through a long course of original investigations, but by grasping hastily at all statements and dogmas that are afloat respecting it, seeking to participate in its treasures as an inheritance from strangers, rather than by examining into its foundations and building up its structure: this is the reason that we find even more dangerous prejudices to combat in science than in practical life. From the very nature of theoretical science, which escapes the continual tests and trials which are applied in practical matters, it happens that mere tradition and well-pursued investigation, old ideas and recent advance, falsity and truth, long remain side by side. Hence prejudice and misconception exist longer in science than in life. Thus it is that the farther a science is removed from contact with the business of life, and the farther it traces back its origin towards the middle ages, the more likely it is to be treated on the senseless method of developing the science through philological discussions. Thus it has been with Botany: books have been written when plants should have been examined, conjectures have been made when investigations should have been pursued. Hence for about a century we have but revolved in a circle, without making the least advance or discovering new facts; and new laws are given us which are only the result of the play of chances, whilst correct fundamental maxims and correct methods of advance would have guaranteed the solution of various problems, and secured the progress of the science.

My aim is to establish the necessity of embracing, as a fundamental principle in the study of the whole, the existence of an essential life in each separate cell. Hence arises the necessity of carrying on investigations in the first instance in the individual cells, or in portions of the vegetable structures, in which we have to do with few cells in combination. On these we must make our first experiments, and from them draw our first conclusions, which we may then proceed to apply to subsequent investigations into the general structure of the plant, pursuing all our inquiries with the aid of the microscope, and placing them under the control of an accurate history of development. Upon such a plan alone can we make a sure advance in the study of vegetable life.

For want of such a plan little or nothing has hitherto been done. It is hence a consequence that all foregoing physiological experiments, and their

results, are and must be almost worthless, because they fail in fundamental maxims and correct methods of research, and in the smallest as well as in the greatest matter it will be necessary for us to recommence our investigations.

After this recapitulation and reference to former paragraphs, it now only remains for me to point out the questions to be investigated, and the experiments to be made, in this department of our inquiry.

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# CHAPTER I.

## GENERAL ORGANOLOGY.

## SECTION I.

### GENERAL PHENOMENA IN THE LIFE OF THE ENTIRE PLANT.

### A. *Of the Life of the entire Plant.*

§ 185. The life of the plant, as of the elementary organs, is seen, in even the process of formation itself, to be nothing else than complex physiological and chemical processes, which are connected with a special form. Here, then, well-known physical and chemical powers must be studied. In general we know but little of these in relation to the plant, and of some nothing at all. Heat and light, as necessary conditions of all or of many chemical processes, are also conditions of life in the plant, but in various degrees. Some *Algæ* and *Fungi*, as *Protococcus nivalis* (the so-called red snow), appear at 0°; others can live in the dark, as *Rhizomorpha subterranea*, *Tuber cibarium* (truffle); others need a high temperature, as many tropical plants, or intense light, as many alpine plants.

We are unacquainted with the action of electricity and magnetism.

The life of plants is, in the highest degree, dependant on the life of the whole earth. Fixed to a particular spot, or if unattached, as is the case with some floating plants, yet without power of spontaneous movement, they must receive all that they require to support their vital phenomena from without. This dependance is especially seen in the means of reproduction. The dispersion of the spores, the transferring the pollen to the stigma, &c., is frequently entirely dependant upon external circumstances, such as atmospheric moisture, wind, motion of the waves, the life of insects, &c.

On the process of formation, so far as it is connected with the existence of the entire plant, I shall speak later under the head of reproduction.

Our present business is the observation of the physico-chemical processes as they are found in the individual elementary organs, or in the groups of the same, called *tissue.* What has been already said in the First Book will hold good here also; and we have now to consider how sometimes, through the process of formation in the entire plant, special modifications appear in the sum of the phenomena of the life of individual cells. These are, however, but little known to us. Heat and light, which are essential to many chemical operations, appear to act upon the entire plant in no other way than upon the sum of the cells. The influence of electricity and magnetism upon the cells is as little known to us as is the operation of these agents upon the entire plant; notwithstanding, electricity appears to play an important part. On this subject there are some vague observations in Froriep's Notizen (vol. xix., No. 9., Aug. 1841.), by Thomas Pine. Instead of indulging in conjectural fancies, I will here propound some queries, which will not appear idle since they require solution. Does a tree in which vegetation is vigorous, or yet better a vegetating *Musa,* or the same in tropical climates, exercise any influence upon a magnet suspended near it? If a *Chara* were made to grow so that it should be spirally surrounded by a continuous galvanic stream, which should be either parallel or at right angles with the direction of the ascent of the sap, would it suffer any change in its vegetation, and what?

The dependance of the life of the plant upon the life of the earth is in the highest degree interesting. We must here assume, that in the agencies on which the meteorological phenomena, the formative principle in the embryo, &c., depend, is to be found the cause why, at the blooming time of a particular plant, a particular kind of insect is produced, whose life again depends upon the nectar in the flower of the plant, and by the sucking up of which the transference of the pollen to the stigma is effected. For particular plants other agencies are needed; as, for example, it is requisite that wind should occur at the flowering time of the *Abietineæ,* that there should be undulatory motion of the water at the time of the flowering of the *Vallisneria,* and rain with the development of the capsules of *Ambrosinia Bassi.* These phenomena may appear accidental, but they are necessary consequences of the primary powers which are seen in the formative processes of the earth. The rain could not fall at the appointed time, and under the existing circumstances, without at the same time causing the internal formative energy of the earth to bring forth an *Ambrosinia;* and the meteorological relations would at the same time be so arranged, that on the developed spathe rain should fall. The spathe of the *Ambrosinia* is boat-shaped, and floats upon the water. By means of the capsule, whose wing-formed appendages, uniting with the spathe, form a little cavity, the spathe is divided into an upper and under chamber. In the upper one is found one single ovary, in the under one exclusively the anthers. The pollen cannot reach the stigma without the assistance of rain, which filling the under chamber and the half of the upper one, lifts the floating pollen to the level of the stigma, and hence the pollen-tubes can pass along. This may be taken as one of the least known examples of the dependance of plants upon the assistance of external natural phenomena. The operations of wind and weather are more generally known, as also is the aid rendered by insects, on which subject we find some interesting observations by Conrad Sprengel, on the Secrets of Nature discovered in the Structure and Impregnation of Flowers; Berlin, 1793.

### B. *Germination.*

§ 186. Germination (*germinatio*) has a very different signification in Cryptogamic and Phanerogamic plants. With the first, as also with *Rhizocarpeæ*, it is the development of a single cell, separated from the mother plant, to an entire new organisation; a process which corresponds in the greater part with the formation of the embryo in the Phanerogamic plants. Of these processes we know nothing further than what may be considered analogous to the life of individual cells. That which is most difficult to explain here is the same as in the *Phanerogamia*, namely, the reason why the spores remain so long without exhibiting signs of vital activity. In *Phanerogamia* germination is only the development of an already organised embryo into the perfect individual. The continued development has no essential difficulties; but the circumstance of an inactive vegetation previous to germination is the reverse of this. We find here the following circumstances take place. Together with the gradual maturing of the embryo, its cells are gradually filled with assimilated matters, as starch, oil, and mucus, and they lose by degrees almost all their watery particles; hence arises a condition in which, on account of the failure of moisture, the chemical changes, and with them the vital processes, are slowly effected. This condition remains in different plants various periods of time, and is capable of being with some of them prolonged for even a thousand years, or more, without the seed losing its capability of development. This tendency to development is not aroused by some circumstances which would be sufficient to excite the actual vital processes of the plant. Thus the seeds of the *Cerealia* will endure exposure to water at 45° C., watery vapour of 60° C., in dry air of 75° C., and in dry cold of 50° C.* That with the commencement of germination, the accession of moisture, &c., gives activity to chemical changes, is far less striking than is the fact, that they have not already taken place; but no one has ever dreamt of discovering the cause of this latter.

The phenomena of germination are as follows. The coverings of the embryo (the testa, and, where present, the albumen and pericarp) swell up under the influence of water pressing in; then the cells of the embryo become distended, at first especially those of the radicle and the lower part of the cotyledons (called *cauliculus*); by this means the radicle is forced from the bursting seed, it sinks into the soil, and whilst fastening itself in it, the slight curve of the axis is removed by the distension of the cells lying on the concave side, and the embryo erects itself above. The distension of the cotyledons then forces off the coverings, which at length fall away, and the free young plant grows unimpeded. Usually in Monocotyledons, and occasionally in Dicotyledons, as, for example, in *Nymphæa*, *Quercus*, *Æsculus*, &c., the inferior part of the cotyledons

* Edward and Colin in Ann. des Sc. Nat., 2d ser. Bot. i.

is so exceedingly distended, that the plumule is pushed from its coverings and unfolded, whilst the summit of the cotyledons have not yet left their envelopes. Where albumen is present, the cotyledons often grow so rapidly within the envelopes, that they consume all the albumen, whilst the entire embryo in the mature seed takes up but a very small portion of space within it. Unimportant varieties in particular seeds are almost countless, and almost every seed in germination exhibits its own peculiarities.

With regard to the vital processes during germination, two phenomena are to be distinguished, one of which has nothing to do with the growth of the plant.

At the time of the maturing of the seed, the cells of the embryo-sac are usually filled with assimilated matter, whereby its shrinking from the constant loss of water is prevented. The greater proportion of this matter is not needed for the nourishment of the young plant, and is subsequently destroyed, whilst the carbon of the starch, oil, &c., is consumed at the expense of the atmospheric oxygen taken up into the plant with the water, and is liberated in the form of carbonic acid gas, whilst hydrogen and oxygen combine to form water, and during these processes heat is given out. By this means the cells become once more furnished with fluid contents, and an active chemical life in their interior is again rendered possible. The next consequence is the conversion of the remaining substances into gums and sugars, which are then employed for the formation of new cells. Mucus, as a catalytic substance, is doubtless active in the processes.

A similar process to that in the embryo goes on in the albumen, and the nutritious matter thus prepared is supplied to the embryo through its surfaces. In many embryos, especially those of Monocotyledons, the cells of the cotyledons become quite papillose, and unite closely with similar papillose cells projecting from the inner surface of the albumen.

The testa, and the fruits enclosed in shells, according to some specific peculiarity of their structure, sometimes exclude the entrance of water, and so retard the process of germination; and sometimes, on the contrary, they accelerate it.

We have already spoken of the morphological phenomena of germination; observations here have been so imperfect that they are of little scientific value.

We know nothing at all respecting the cause of the direction taken by the germinating plant. Immediately the plant is exposed to the light, it developes in its external parts chlorophyll.

In order to understand the subject of germination, we must know the structure of the seed. We find that it contains the rudiments of the future plant, namely, a small body, having as essential parts a radicle and a terminal bud. To these are added supplementary organs, which are used at the end of the process of germination. These supplementary organs are either the first leaves (cotyledons) or the albumen. In these we trace three distinct relations, by means of which they subserve the purpose of re-

taining the activity of the embryo until the time comes for its development. Their cells contain either less mucus but more starch, as in the leguminous cotyledons, and in the albumen of the *Cerealia;* or they contain more mucus and, instead of starch, a fat oil, as in the cotyledons of the *Cruciferæ* and in the albumen of some Palms and *Euphorbiaceæ;* or lastly, they contain scarcely any mucus, but their walls are strikingly thickened, and the cellulose is found not to possess its usual physical condition, or is in some way chemically distinct. It is more easily dissolved and decomposed than usual. This is seen in some leguminous cotyledons, as, for example, in the Tamarind, in the albumen of many Palms, as the Date-palm, and in a most striking degree in the Ivory-nut (*Phytelephas*). From this it results that we have six principal conditions, without mentioning the intermediate states, which demand an accurate investigation. Hitherto no microscopic and chemical history of germination has been given with any accuracy or completeness; we are still in the infancy of our knowledge respecting it. For the most part, chemists understand nothing of microscopic physiology, and botanists little of chemistry. Hence there has been no harmonious pursuit of science between them, the absence of which has retarded both, so that we neither possess, nor are on the eve of possessing, a complete and fundamental knowledge of the history of germination.

The reason of our ignorance on this subject arises from the fact, that in investigating it the chief attention has been turned upon that point where the difficulty does not exist. The development of the young plant will be explained when we shall have explained the life of the plant in general. The principal difficulty that requires explanation is how the conditions, which in an embryo result in a definite process, remain for a long time suspended. If we place a ripe acorn in the soil, under all the circumstances requisite to germination, why do not those chemical processes which excite germination and development immediately take place? In this case chemical processes slowly go on in the interior of the cells, with which we are as yet altogether unacquainted; and perhaps, also, the structure of the cells, or the chemical nature of their contents, is such as to make the operation of external agencies only very slowly effective. The Coffee-bean does not germinate at all, unless it is placed in the requisite circumstances immediately upon its ripening. Wheat has been proved, by the experiments of Sternberg, to germinate after it had lain inactive for three thousand years.* Many facts must be collected, and the most minute chemical investigations must be made respecting the contents of the cells and the cell-walls, the structure of the embryo must be accurately examined, before we can obtain correct results: all else is but theoretic dreaming. Only confusion or uncertainty can be expected where so much, if not all, is yet to be investigated.

Thus much, however, we have ascertained teleologically, namely, that the cells of the embryo and the albumen are completely filled with assimilated matters, in order to prevent, during the drying of the cells, their crushing together, and thus to make their future active life possible. Of these matters, a considerable portion is not only superfluous to the support of the life of the embryo, but is actually in the way, and when germination commences it is disposed of by being converted into carbonic acid and water. To this atmospheric oxygen is essential, and also, as in every other chemical process, a certain amount of heat and moisture, and these

* He made wheat taken from the coffins of mummies to germinate, and the same has been done in England. [The circumstances under which this has taken place, in England at least, are not free from suspicion. — Trans.]

are the so-called conditions of germination. The measure of each which is necessary varies with the different kinds of seeds, according to the chemical nature of the contents of the cells, of the cell-walls, and their general structure.

Water plants germinate best in water,—land plants in damp earth. Of the precedents of this process we know nothing at all. We do not even know all the conditions under which starch is produced and decomposed; and those with which we are acquainted agree so little with those presented in the germinating plant, that they can serve little towards the explanation of the matter. The discovery of diastase by Payen and Persoz made a great noise, and it was generally thought that the key had been found; but it was forgotten that diastase only dissolves starch at a temperature of from 65°—70° C., and this temperature is not found to exist in germinating plants, and, should it be produced, it must destroy life. It is clear that only the decomposition of the carbonaceous substances is essential to the process of germination; all remaining phenomena belong solely to the processes of vegetation which appear later.

A more important point occurs here, namely, the direction which the germinating plant takes. The examples of *Viscum* and *Loranthus* prove that it is not a universal law of vegetation that the root should grow downwards towards the centre of the earth, and that the stem should take a contrary direction. With the generality of plants this is indeed the ordinary manner of growth. However the seed may chance to fall, yet, in germination, the radicle so bends itself as to sink perpendicularly into the soil, whilst the stem rises perpendicularly from it. The direction which the stem takes is, however, much modified by the influence of light; it is found to grow in the direction from which the light comes: hence, if the light falls obliquely, the stem rises in a corresponding direction. Many theories have been invented to explain this, and supported by the very interesting experiments of Knight *, gravitation has been called into aid; this only proves with what obscure notions some persons are satisfied. Whether the experiments of Knight would always give the same result is very doubtful; but were it so, they would yet be very insufficient to establish that gravitation is the cause of this phenomenon, seeing that *Viscum* and *Loranthus* would not fall within the law; and the causes which determine the direction of the growth of these plants are probably the same as in others. Gravitation on the earth is in proportion to the mass and volume. These are sometimes greater in the radicle, sometimes in the upper part of the embryo; hence, according to the usual law of gravitation, the plant would sometimes grow in one way, sometimes in the other, which does not happen. Moreover, as the radicle lengthens, it draws fluids from the soil, and the contents of its cells are always more dilute and specifically lighter than those in the upper parts of the plant; hence it would turn the root round, which being attracted least to the earth, would ascend into the air. A cone falls to the earth upon its base; we have embryos of conical form, as well as of other forms, but both germinate so that the radicle sinks into the earth, though it may be projected from the point or base of the cone. No embryo germinates free, all remain for a longer or shorter time enclosed in the testa or pericarp, from which the embryo for some time only projects a small point: gravity

* Treviranus, Beiträge zur Pflanzenphysiologie (in which the works of Knight are translated). Göttingen, 1811, p. 191.

must then act upon the pericarp, and thus determine the position of the embryo. In short, without consideration, an imprudent word has been thrust forward, and supposed to afford an explanation. I have already observed that no botanist is justified in saying absolutely and without reason how much or how little he will adopt of other systems for his own use, or as a point to start from. When he avails himself of other sciences, he must clearly comprehend the notions of these sciences, or he will but make himself ridiculous. But when, in the nineteenth century, a professor of physics can so err in fundamental principles as to say "action from contact is improbable, because we know no example in which a body at rest can set another body in motion," more at present can scarcely be demanded of botanists.

It would be too much to assert the impossibility of gravitation being the cause of the phenomena above mentioned; but we have nothing to do with the power of gravitation, because we have no object on which it could act.

The various fancies respecting the peculiar vessels which are employed in conveying the nutritive matter from the seed-leaves to the radicle, and all similar theories which are found in old works, I have left without notice, for they are altogether worthless. I will, however, enumerate some of the matters demanding examination, which will afford a more intimate knowledge of the processes of germination.

I. An explanation of the cause why, in the embryo and the albumen, the starch is dissolved and the oil of fat is decomposed.

II. An accurate determination of the degree of heat present during germination, and a comparison of the same with the quantities of carbon and hydrogen which are consumed.

III. An exact quantitative analysis of germinating plants, and of their separate parts in all stages of germination; with an exact quantitative determination of the proportion of water taken up, and of gases interchanged, as well in embryos containing starch as in those containing oil. It is evident that such analyses must be constantly pursued with the help of the microscope.

IV. A repetition of the experiments made by Knight, with a view to ascertain whether the germination and continued growth might not be made in a direction the reverse of that which is usual, if earth should be placed upon them from above, whilst they should be subjected to strong light from below.

The development of the spores of Cryptogamia, which is also termed germination, finds no analogy here but with the development of the pollen-grains in the embryo. In each of these, however, the physical and chemical conditions are different, and a special investigation of the process of development, with respect to the chemical and physical conditions of germinating ferns, is much to be desired; but there are many preliminary difficulties to be overcome. A close investigation of the kind pointed out in the third section above would tend to the explanation of many of the laws of vegetation, if it could be followed out with a number of the *Algæ*, for instance, *Spirogyra*, and in this case the natural position of the plant would greatly facilitate the investigation.

## C. *Of Growth.*

§ 187. Growth of plants generally is the increase in their volume and their mass. In the scientific treatment of the subject, we

must distinguish three several processes, namely, growth in the narrow and literal sense, that is, the formation of new cells; the unfolding or extension and enlargement of cells already present; and the lignification or thickening of the cell-walls by spiral and porous layers. Each of the three contributes in different ways to the perfecting of the entire plant and its organs. It is especially important to distinguish the first and second of them precisely. The process termed germination is marked by two periods, the first of which consists in the softening and extension of cells already formed, and the second in the formation of new cells. The rapid growth of the *seta* of *Jungermannia* belongs to the process of unfolding, also the extension of the internodes in the Phanerogamic plants. But here we greatly need exact and comprehensive investigations.

Essential growth goes on, so far as is at present made out, by the formation of new cells in the interior of the old or parent cells, which, by resorption, set the new ones free. No other mode of increase of the cells has been as yet fully established.

I have already asserted*, and I believe I have made it clear, that there can be no scientific treatment of the vitality of plants without an accurate distinction between the three above-mentioned phenomena, and in every case an apprehension of which of the three is actually present. This is so simple, that when once attention is called to it, it will be understood, for examples of the three kinds of growth must be known to every botanist.

By attention to the first and second division, we obtain a distinction of two essentially different periods in the development of every part of a plant; first, the period during which the cells which constitute its substance are formed; and secondly, when they become expanded. The two periods are often very accurately separated from each other, as, for example, with many petals; in other cases the one passes into the other, as in the anthers.

In botanical books a number of examples are given of periodical accelerations or retardations of growth.† All these examples are useless for the derivation of laws, because the previous distinctions have not been at all attended to. Treviranus, for example, quotes the rapid reproduction of the anthers in an ear of rye, when they have been stripped off by passing through the mouth. In this case it is only a question of the distinction of previously existing cells; the same also with respect to the development of the flower-stalk of the *Agave*. Thus the investigation of E. Meyer on barley and wheat (Linnæa, vol. iv.), and of Mulder on the leaves of the *Urania speciosa* (Bydragen tot de naturk. Wetensch. vol. iv.), with respect to the comparative growth by night and by day, and at the varying hours of the day, are useless, because no distinction has been made between the formation, and the mere expansion of the cells. To this branch of the subject properly belongs all that has been said upon the distinction in the growth of the stem, the root, the leaves, and all other parts (see Treviranus, Physiologie, vol. ii. pp. 152—179.). All experiments and observations that have

* Müller's Archiv, 1838, p. 158.; Beiträge zur Botanik, vol. i. p. 141.

† Treviranus, Physiologie, vol. ii. p. 442.

hitherto been made, without reference to these essential distinctions, are useless, and must be followed out anew if they are to serve for the extension of our knowledge of vegetable life.

In germination, the above distinctions are definitely marked; it yet remains for us to follow this out more accurately by the investigation of the previous chemical changes in the germination of *Phanerogamia.* I believe that the simple softening and expansion of the cells continues as a first stage until the time comes when the root projects itself into the earth; then new cells are formed, probably first at the apex of the root, and then in the plumule. In the germination of *Cryptogamia*, where the development of the reproductive cells continues uninterruptedly, without giving any time for the repose of vegetation, no such periodicity is observed.

The most important point which here presents itself is the mode of increase of the cells, and the proper growth of the plant. Investigations on this subject are especially wanted. I was the first who (in Müller's Archiv, 1838) sought to investigate this matter, and thereby to establish a foundation for further inquiries, the necessity for which had scarcely, up to that time, been foreseen. At the same time appeared Schwann's treatise, with the same object, on animals. Immediately there arose a dispute, not upon the correctness of the facts given, but upon the importance, or not, of such a foundation for the study of physiology and histology: others desired to wear the laurels which Schwann had gathered. Soon, however, a new and strikingly active life, proceeding from the foundation laid by the discoveries of Schwann, appeared in physiology; and thus first my name was mentioned in friendly union with his.

This is not the place to enumerate the splendid results which were thus obtained by both physiologists and botanists. Almost five years have gone by since the appearance of my work, and not a single botanist has found it worth the trouble to repeat my investigations, conducted with so much care and labour, in order either to confirm or to confute them.* This circumstance seems to me to justify some of the harsh observations that I have made upon the state of botanical science, since it shows beyond dispute that we have failed not so much because of the difficulty of obtaining results as from the want of the scientific spirit which would seek after them. There are honourable exceptions; but with the generality of botanists, even down to our own times, the necessary possession of a few dried fragments of plants, and a superficial physiology acquired by peeping through a microscope, is called science; to-day this, to-morrow the contrary, the day after the same as the first; and all this because they make no fundamental or comprehensive researches, and are without the conditions of a scientific induction: and at the present day this is called seeking for the truth! God save the mark! In the past year, however, a preparation has been laid for a more fertile future, chiefly by young, vigorous spirits, who, having pursued zoological studies on true principles, have introduced the same scientific method of investigation into their botanical researches. The time is evidently not far distant when no botanist will presume to dictate on the science as long as he has not made fundamental investigations upon cell-development.

* An exception must be made in this country, at least, in favour of my friend and assistant in the translation of this work, Mr. Arthur Henfrey, who has repeated with much care the researches of the gifted author, although he has not been able to confirm all his views and observations.—Trans.

We owe many thanks to Nägeli for some communications containing very able observations (Zeitschrift für wissenschaftliche Botanik, Pt. I.). The writings of K. Müller, in the Botanische Zeitung, are also valuable; and in the labours of Hartig, and other such, we recognise pleasing signs of a better time, though with some of the results which Hartig supposes he has obtained I cannot agree.

The doctrine of the formation of cells is treated of § 14.

§ 188. It has not yet been discovered how far the various parts of plants, or the various groups of plants, present various kinds of growth. Accurate investigations are wanting on this subject. So far as this condition influences the form, or the change of form, in plants, it has been already treated of in Morphology.

In the animal kingdom the phenomena of reproduction and growth stand in close connection. Under the term reproduction, used in this sense, is to be understood a new formation to supply a part that has been lost, in the same place, and of the same form. There is, probably, no such reproduction in the vegetable kingdom. A part of a plant which is lost is not restored by the reproduction of a corresponding member; but, on the contrary, the process of the healing of wounds from loss of substance takes place frequently by the filling up of the existing breach with a substance similar to cork.

Of the varieties of the processes of vegetation in various plants, or parts of plants, we have at the present moment nothing to say. I have already, in speaking of the formation of the pollen, called attention to the opinion of Nägeli. The special parent-cell is always formed in the interior of another cell; but this mode of formation is different from that earlier described. Nägeli found it frequent in the *Algæ*.

Respecting the peculiar chemical processes of individual groups of plants, we know nothing. In the indefinite growth of the entirely independent individuality of the plant there can be no reproduction in the same sense as the reproduction of the tail of a lizard, &c.; for the individual embraces a definite circle of forms, but not a definite number of forms, and never produces all its essential organs at the same time: so that the loss of a member may be replaced in a plant, but it cannot be through the restoration of the same form in the spot from whence it was removed, but by the formation of a similar organ in another place. The loss of certain organs in plants, and the formation of corresponding organs in other places, is quite conformable with the general laws of vegetation, of which we have earlier spoken. The tree, for instance, that loses its leaves in autumn, forms new leaves in spring from its buds; but each bud is an essentially new individual, which consists of perfectly-formed stem and leaves; but it is developed upon the remains of a former individual, and is vitally united to it. Internodes that have lost their leaves never throw forth new leaves, which grow rather on new internodes, and thus belong to a new individual. But two examples have as yet come to my knowledge wherein there has appeared to be a reproduction in the same place of one and the same part which had been lost. One of these occurred in a plant belonging to the family of

*Algæ*, which we have not yet discovered to possess morphologically definite organs.

According to the observations of the senator Dr. Binder, it is not infrequent to find in *Laminaria digitata* and *saccharina* that a new cell-formation is organised upon the edges between the under stalked part of the plant and the upper flat extended surface, from which the formation of an entirely new upper flat part of the plant is produced, whilst the old parts are at the same time destroyed. In the excellent collection of Dr. Binder, I saw a number of instances of this process in its different stages in the *L. digitata.*

The other case appears to exist in the *Ceratophyllum*, in which single leaves are eoccasionally cast off about two lines above their origin, and again produce from the stump a perfect leaf. I have already made known this fact in my contributions to our knowledge of *Ceratophyllum* (Linnæa, 1837)

The healing process is very general in the vegetable world, and the substance which is produced for the purpose is similar to suberous tissue (cork), which I have fully described in my paper upon *Cacti.* But this subject belongs rather to the pathology of plants.

## D. *The Process of Nutrition.*

§ 189. The collective nutrition of the plant embraces various different processes, by which foreign matters are received into the organism, are entirely or partially appropriated, and through which that portion of such matter which is not fitted for the nourishment of the system, or which would impede the vital processes, is thrown off. These processes are physical, so far as regards absorption and excretion; chemical, so far as the changes produced in the substances; and morphological, so far as they are concerned in the fixation of the appropriated matters in definite organic forms. With plants which are not furnished with special physiological organs, we cannot pursue the subject of nutrition according to the function of individual co-operating organs. Each cell is nourished according to its own special nature, and in different ways. In studying the nutrition of the plant, we must, in the first instance, observe separately the physical, chemical, and morphological processes; secondly, the varieties of the first, according to the different nature of the media surrounding the plant or its parts; thirdly, distinguish the following peculiarities of the physical and chemical processes in the entire plant—for instance, an essential vitality may exist in the individual cells of a plant, and certain processes may be carried on within them without producing any effect upon the neighbouring cells, and upon the entire plant, whilst processes carried forward in dead cells of the plant may exercise an important influence upon the surrounding living cells, and thus upon the entire plant; lastly, the distribution of the absorbed matters in the entire plant must be kept in view.

From the preceding paragraphs it will be evident that the old analogy between the absorption of food and the processes of assimilation, respiration, secretion, and excretion in animals and plants, will not hold good. We are not indeed able at present to supply its place according to the requirements of organology from a more simple and correct point of view, for we have but single facts to deal with, and they are too few in number to enable us to unite them into a system free from objections. It is easy enough to see the fallacy of the analogy hitherto supposed to exist between certain processes in the animal and vegetable organisms; but it is most difficult, and at present impossible, to substitute a new arrangement of facts, because here, as everywhere else, we are surrounded with a vast mass of useless investigations, and are almost totally unprovided with serviceable materials on which to found a basis for our theory. Men have contented themselves by drawing out romances and theories, the mere offspring of fancy, supported only by the slightest and most superficial phenomena; and even in our own century there is carelessness and crudeness about our physical and chemical investigations which savours very much of the ignorance of the middle ages. The most senseless experiments have been made in perfect ignorance of physical, chemical, and physiological facts, and on the supposed results obtained from them false theories have been put forth. Experiments in which plants have been placed in pulverised marble with water saturated with carbonic acid, and from which has been deduced the supposed fact that carbonic acid is unfit for the nourishment of plants, are as senseless as if a zoologist should feed an animal with strychnia, and should thence make the deduction that food containing nitrogenous matters is not wholesome.

Experiments upon the phenomena of life in plants can only be of value when performed in one of two different ways: either the plants on which they are made must be allowed to vegetate under all their natural circumstances, means being taken which shall enable us to observe the processes going on in them according to time, measure, and weight; or else we must compare the phenomena of vegetation according to time, measure, and weight in a plant excluded from one or more natural conditions, with the same phenomena in a plant placed under natural circumstances. Both kinds of experiments should have only one end in view, the understanding of the phenomena of life; and yet we shall not succeed unless we subject the elementary matters and powers which exercise an influence on the plant independent of itself, to an accurate investigation, and understand thoroughly the peculiarity of their action. Since the time of De Saussure innumerable experiments have been performed to ascertain the capacity of plants to select their own nourishment; and the theories and consequent contentions upon the subject would fill a small library. It appears to me, at least since the discovery of Dutrochet, that all disputes upon this subject are useless, until we have ascertained whether the organic or the inorganic matter present in the plant may not, independently of the life of the plant, exercise a power of affinity, and how far this harmonises with the phenomena already observed in the plant.

The question must be thus placed: how do albumen, gums, and sugar behave in the endosmotic apparatus towards a number of soluble salts; and how would they behave if many of these salts should be mixed with them? The salts used in this case should be such as are commonly diffused in water and on the earth. If we, therefore, allow plants, in

which we have accurately examined the contents of the cells of the roots, to vegetate in the same mixture of salts, we may thus ascertain how far the simple absorption, as to quality and quantity, is affected by the mere mixture of albumen, gum, and sugar in the interior of the cell. We have not such experiments to adduce, or at least very few; and we must confess that with respect to the nutrition of the plant we know scarcely anything. Part of this subject belongs to morphology; the materials which remain we may arrange under the following heads: —

I. The nutrition of the plant in general.
II. The absorption and excretion of the nutritious matter.
III. The assimilation of the nutritious matter.
IV. The external conditions of absorption and assimilation.
V. The motion of the sap in plants.

## I. *The Food of Plants in general.*

§ 190. The four elements which are essential to the formation of all organised substances, namely, carbon, hydrogen, oxygen, and nitrogen, are found in continual circulation in nature. We find them in union with organic substances in the vegetable world. The animal kingdom is entirely dependant upon vegetation for support, either mediately (as the carnivora) or immediately (as the vegetable feeders). By means of the vital functions of animals (as respiration and perspiration), and by the corrupting and putrifying of their excrements, as also by the death of animals and plants, and, finally, by the process of burning, organic substances are continually converted into water, carbonic acid, and carbonate of ammonia, which, as purely inorganic combinations, are held by the atmosphere. These are again exclusively appropriated by the vegetable kingdom, and restored to the domain of organised matter.

In an inductive inquiry into natural objects, before all things we must strive after the discovery of leading maxims, which should be securely founded, and by which we may decide upon the admissibility of hypotheses, and through which alone science can be made free from fiction.* The paragraph above is a leading maxim of this kind, concerning the changes of matter which go on in the three kingdoms of nature. In

* In the following remarks a number of authorities will be used, and, in order to avoid further reference, I have once for all given them here: —

1. Humboldt's Reisen, and Essai sur la nouvelle Espagne.
2. Codazzi, Resumen de la Geographia de Venezuela.
3. Darwin's Voyage round the World.
4. Blasius, Reise im Europäischen Russland.
5. Ure, Dictionary of Arts.
6. Macculloch, Dictionary of Commerce.
7. Liebig, Organic Chemistry, in its Relations to Agriculture and Physiology.
8. Boussingault, Economie rurale.
9. Loudon, Encyclopædia of Agriculture.
10. Essays on German Agriculture, by Block, Schwerz, Schweizer, Hlubeck, &c., in the Handbuch für angehende Landwirthe, by J. v. K. Leipsic.
11. Lastly, I have used many private communications on methods of culture from travellers and natives of Germany.

recent times this has been called Liebig's theory of the nutrition of plants: but this is doubly wrong, for in the first place it is no mere theory of the nutrition of plants; and in the second place, it did not originate with Liebig, but with Priestley, and has been gradually developed from his time by the most distinguished experimentalists. Liebig has, indeed, in recent times dwelt upon the importance of its universal recognition, and its relation to the development of a true physiology of plants. He has also done great service by working out the whole problem upon a new method, which was first introduced into the natural sciences by Alexander von Humboldt.* This method consists in disregarding at first individual and unarranged observations†, and directing attention to the great mass of the phenomena of nature, and where the deficiencies, on account of their great number, attain a minimum of importance, to make calculations, which may be made the basis of points of departure, alike in the estimate of the value of the smallest as of the most isolated part.

But on account of the great influence which leading maxims exert, comprehending, as they do, not only facts and groups of facts, but entire circles of hypotheses, it is above all things necessary that they should be placed on a secure footing, and be susceptible of the strongest possible proof. To the most common examples belong the asserted constancy of the composition of the atmosphere, which Liebig has frequently put forward in the fore-ground. "Respiration and combustion consume an immense mass of oxygen, yet the quantity of oxygen in the air remains the same; consequently the vegetable world appropriates the carbon of the generated carbonic acid, and again sets free the oxygen."‡ If we need proof of this view, we have the following: — A man in the course of a year changes 225 lbs. of carbon into carbonic acid, so that a thousand millions of men would consume 2250 millions of centners§; for all the animals‖ on the earth we may take double this quantity: thus, in the whole, 6750 millions of centners of carbon are yearly burned, which, during the process of burning, would consume 1800 millions of centners of oxygen gas, to which may be added about 400 millions of centners for the burning of coal.⸸ The remaining processes of combustion would give 1500 millions of centners of carbon, which consume 4000 millions centners of oxygen. Hence we may take the consumption of oxygen in the course of 300 years at 660 billions of pounds, or about $\frac{2}{10}$ths of the present contents of the atmosphere; and this would fall within the oscillations of our eudiometrical calculations, if we had observed them as accurately 300 years ago as at present.¶

* The talent which forms an epoch in the history of the natural sciences consists not in the discovery of individual facts or laws, but in the introduction of new ways, the discovery of new methods.

† To what absurdity and charlatanerie a dwelling upon individual facts, without a comprehensive view, may lead, has been recently seen, in the most forcible manner, in the work of C. H. Schultz, on the Discovery of the true Food of Plants.

‡ According to Liebig, man consumes daily between 17 and 27 ounces of carbon.

§ A centner is about 100 pounds.—Trans.

‖ Boussingault calculates the horse consumes 158¼ oz., and the cow 141½ oz. daily.

⸸ According to Ure, 677½ millions of centners of coal contain 71 per cent. of carbon, which is equal to 481 millions of centners of carbon.

¶ At my request, my colleague, Professor E. Schmid, had the goodness to calculate

All these calculations are much higher than those given by others, but, as will be subsequently shown, are far within the truth. About the pretended constancy of oxygen in the atmosphere, nothing has as yet been established. As the calculation stands, only the contents of the carbonic acid in the air are regarded. According to the above data we receive annually into the atmosphere, through the processes of respiration and combustion, about 30,000 millions of centners of carbonic acid, or in 5000 years 15,000 billions of pounds. Unfortunately we can hardly approximately estimate the out-pourings of volcanoes, but they certainly cannot deliver much less carbonic acid than respiration and combustion; thus there ought to be from twenty to thirty times as much

afresh the contents of the atmosphere, as the above did not satisfy me. The following are the data on which his calculations were based: —

For the determination of the mean height of the barometer, twelve determinations (Berghaus' Physical Atlas) upon the surface of the Atlantic Ocean were taken, the result of which was (the attraction of the earth reduced to 45° latitude) —

$$=336''', 973 \text{ Par.}$$
$$=348''', 76 \text{ Rheinl.}$$

The pressure of atmospheric vapour was taken, according to Dove, at a yearly mean —

| | |
|---|---|
| at Calcutta | 8''', 350 Par. |
| — London | 4''', 147 — |
| — Jena | 3''', 118 — |
| — Catharinenburg | 1''', 800 — |

The mean would be 4''', 353 Par. But as this number of cases is small, in order to obtain round numbers, 4''', 76 Rheinl. was assumed as the mean. The pressure of the dry atmosphere is as follows: —

| | | |
|---|---|---|
| | 344''' Rheinl. | Mercury. |
| = | 4664''', 364 — | Water. |
| = | 32', 39 — | — |

1 German mile = 1970,1 Prussian rods. (Berghaus, Grundriss der Geographie, p. 5.)

1 German □ mile = 3881294,01 □ rods.

The surface of the earth = 9281916,28 German □ miles. (Berghaus, op. cit. p. 13.)

1 Pruss. C.-F. of water = 66 lb. at 15° R. = 18°, 75 C = $\frac{66}{0{\cdot}998652}$ lb. = 66·089 at 0° C. (Dove, Rep. vol. i. p. 144.)

Thus is the collective weight of the dry atmosphere

$$=1371977266662000000,0 \text{ lb.}$$

The volume of the elements of the dry atmosphere, according to Dumas, Boussingault, and Brunner (Gmelin, Chemie, vol. i. p. 818.) are —

79·16 N.
20·79 O.
0·05 $CO^2$ mean.

According to Berzelius and Dulong, the specific gravity is —

O = 1·1026
N = 0·9760
$CO^2$ = 1·5240

Thus the weight of the elements of the dry atmosphere is —

77·06 N.
22·86 O.
0·08 $CO^2$.

Thus the contents of the whole atmosphere may be calculated as —

| | |
|---|---|
| 1,057245,681689,000000 lb. | N. |
| 313634,003159,000000 – | O. |
| 1097,581813,000000 – | $CO^2$. |
| 1,371977,266661,000000 – | atmospheric air. |

carbonic acid in our atmosphere as we find actually to exist, if some regular withdrawal, a process in nature which consists essentially in the fixing of carbonic acid, does not exist. A similar line of argument might probably be pursued with regard to ammonia. The example, as given by Liebig, fails somewhat in this, that he cannot allow that the organic substances of the soil (humus) can arrive at the plants in sufficient quantity to supply their need of carbon, because he proceeds on the entirely false foundation, that the earth receives its water entirely through the rain (which only supplies the smallest part), and only takes notice of the humate of lime, and neglects the generally necessarily present humate of ammonia, whereby the plant might receive more than enough carbon for its consumption. On the other hand, far more easy is the proof, which Liebig only hints at, that if in individual cases there has been a sufficient quantity of humus to supply the plant with carbon, yet there is not a sufficient amount of humus existing to cover the demand made by the whole vegetable kingdom for carbon, a subject to which we shall presently advert.

I maintain that the following mode of research is the only correct one to place securely and make evident the truth of the foregoing view. If we disregard entirely any definite geological hypothesis, yet we must admit that the earth has a history of its origin which I will attempt here to sketch. Before their creation there could be no organic substances. Now, for the creation of these there are only two conceivable conditions: either there was at once created a definite quantity of organic matters, or these were formed gradually and continuously out of inorganic substances. All the organic substance that the plant derives from the organic matters of the earth, the first hypothesis, proved or unproved, supposes to occur in the following way: there is a certain quantity of organic matter which constantly circulates between the animal and vegetable kingdoms; the products, excretions, and dead bodies of the one kingdom supplying nourishment for the other. *A priori*, this view has nothing in it improbable, but according to experience it is impossible, as the processes of life in the animal, decomposition and combustion, interfere. Through these a large part of the organic substances are converted into inorganic combinations. The organic matters must thus constantly diminish, and at length become perfectly consumed. The process of combustion, it is well known, annihilates entirely organic matters as such, and putrefaction and fermentation know no other bounds than the perfect dissolution of organic in inorganic combinations. Lastly, if we look in the process of nutrition at the collective quantity of organic matters delivered in the manure for the culture of plants, we shall find the following*:—

A working horse receives daily—

| | Of dry Organic Matters. lbs. | |
|---|---|---|
| In 15 lbs. Hay . . . | 11·74 | |
| 5 lbs. Oats . . . | 4·07 | |
| 5 lbs. Litter . . . | 3·40 | |
| | 19·21 | 19·21 lbs. |

* In this case the statements of Boussingault are used, but they should be compared with the results of German agriculturists in order to obtain the simplest and most useful averages.

| | Of dry Organic Matters. lbs. | |
|---|---|---|
| Brought forward . . . | | 19·21 lbs. |
| It produces daily— | | |
| In 33·31 lbs. Urine and Fæces | 6·56 | |
| 5·00 lbs. Litter . . . | 3·40 | |
| | 9·96 | |
| Fresh Manure loses when put on the land $\frac{1}{6}$ | =1·66 | |
| | 8·30 | 8·30 lbs. |
| Loss in organic matter from the product of the field to the manure | | 10·91=56 per cent. |
| A milch cow receives daily— | | |
| In 32 lbs. Potatoes . . . | 8·46 | |
| 16 lbs. Aftermath . . | 12·15 | |
| 8 lbs. Litter . . . | 5·44 | |
| | 26·05 | 26·05 lbs. |
| It yields daily— | | |
| 78·28 lbs. Urine and Fæces . | 8·77 | |
| 8·00 lbs. Litter . . . | 5·44 | |
| | 14·21 | |
| $\frac{1}{6}$ loss thereon . | 2·36 | |
| | 11·85 | 11·85 lbs. |
| Collective loss in organic matter . | | 14·2 =54 per cent. |
| A pig of middle size receives daily— | | |
| In 15 lbs. Potatoes . . . | 3·96 | |
| 4 lbs. Litter . . . | 2·72 | |
| | 6·68 | 6·68 lbs. |
| It produces daily— | | |
| In 9 lbs. Urine and Fæces . | 1·28 | |
| 4 lbs. Litter . . . | 2·72 | |
| | 4·00 | |
| $\frac{1}{6}$ loss thereon . | 0·66 | |
| | 3·33 | 3·33 lbs. |
| Collective loss of organic matter . | | 3·35=50 per cent. |

If we make similar calculations with regard to man, for which we have not however so good data, yet, according to the facts communicated by Valentin (Physiol. vol. i.) and Liebig (Organic Chemistry in relation to Physiology and Agriculture), the loss of organic matter in passing through the human body is greater than in any individual animal. How speedily this loss of organic materials is made manifest in the animal is

easily shown by a great example. According to official documents, the stock of cattle in France in the year 1844 comprised of large animals (bulls, oxen, cows, stallions, geldings, mares, and mules) = 10,709,391 st.; of small animals (donkies, calves, foals, pigs, sheep, and goats) = 30,859,454 st. The daily loss of organic matter may be calculated as 11 lbs. in the first, and 3 lbs. in the second class of animals, so that for their nourishment in one year about 76,789 millions of lbs. of organic substances are required, a quantity equal to about six times the weight of the whole of the stock of cattle. If we suppose that the existing quantity of organic matter is 600 times as great as that which represents the whole stock of cattle, yet would the loss during the nourishment of the cattle of France result in a perfect desert in the course of a single century.

It results then from these facts that the organic substances which are burned and serve as food to animals, are at least half destroyed, and that in 100 years they would be reduced to nothing. But we have, both in the history of the earth and in the history of man, in the former from geological period to period, and in the latter from century to century, evidence not of a decrease but of an increase of organic life upon the surface of the earth. There must, therefore, be continually going on a conversion of inorganic matter into organic combinations. From physiological researches* it appears perfectly certain that this cannot go on in the bodies of animals. Neither do we know of any facts in the whole of nature that would lead us to conclude that inorganic substances independent of an organism could be changed into organic compounds. Whilst on the contrary all experience proves that the organic substance is unceasingly passing over into inorganic combinations. The only inference from all this is, that plants convert inorganic into organic substances; and this we must hold as a first great law of nature. The only universally diffused inorganic compounds which can be taken up by plants in order to assimilate carbon, oxygen, hydrogen, and nitrogen, are the carbonic acid gas, water, and carbonate of ammonia of the atmosphere, and from these must the vegetable world be almost exclusively supplied as the materials of their nutrition.† This law concerns not alone the vegetable world in general, but has an important special application in the culture of plants. This will be seen when we look at the production of manure according to the foregoing calculations; and further, reflect that on a well-managed estate a considerable part of the produce, as corn, cheese, butter, wool, &c., is annually taken away, returning no manure to the soil, and that the organic substance remaining

* See Valentin, Liebig, Mulder, &c.

† This thought seems to have floated darkly before the mind of Liebig, when he said "a primitive humus cannot be granted," a proposition to which the sense of the words would give no signification. Under every circumstance, before an organism could be present in the formation of the earth, inorganic must have passed into organic substances, whether as an organic embryo, or as an organic substance from which the embryo would be first developed. As we are ignorant on this point, and are as likely to remain so, as we are with regard to the nature of organic life in the system of Sirius, so is it foolish to assert that either this or that combination could not exist provided it is chemically possible. It may be conceived that, through a special process, dextrin and protein were first formed; and that, during the decomposition of these substances, humus, or even that, favoured by this process of decomposition, the first plant-cell was formed. Thus we might have a primitive humus. With this explanation, the view that no dextrin and no protein are developed independent of an organism may be received, as well as the view now universally held by the most distinguished naturalists, that no specifically definite organism can originate but in a maternal cell, although such might once have originated on the earth's surface.

on the estate must be reduced as food by at least one half. Boussingault places the yearly account of dry organic products contained in the manure in contrast with the products obtained from the soil, during a period of twenty-one years, and finds the proportions are as 33 to 124, so that it would be constantly necessary to replace three-fourths of the humus present, and thus every soil within a short time must be perfectly exhausted of organic matters. According to Sir H. Davy,

| | Organic Matters and Salts. |
|---|---|
| Good soil for the growth of Hops contains | 8·0 per cent. |
| Good soil for Turnips | 0·6 |
| Very good soil for Wheat | 4·4 |
| Extraordinarily fruitful soil | 2·8 |
| Good soil | 1·4 |
| Excellent Wheat soil | 12·7 |

It is thus very clear that the fruitfulness of the soil does not stand in any relation to its contents of organic substances, but that it appears to depend, on the contrary, on the nature of the plants cultivated and the tillage of the soil.

But we are enabled to take quite a different view of the culture of plants, if we do not confine ourselves to the little spot of earth from which our profound agricultural manuals are supplied with material. Loudon gives a view of the kinds of agriculture according to the following scheme: —

1. Agriculture with exclusive irrigation, extending to 35° on each side of the equator.

2. Agriculture with irrigation and manuring, extending from 35° to 45° N. and S. lat.

3. Agriculture with draining and manuring, from 45° to 67° lat.

As the last zone alone embraces any considerable surface of the earth in the northern hemisphere, and as local circumstances, both in the second and third, according to the nature of the plant, determine the use of manure or irrigation, it may be advanced, without fear of contradiction, that generally three-fourths of the agriculture of the surface of the earth is carried on without the aid of organic manures, and that the produce in such districts is much greater than where it is carried on in unfavourable regions by the aid of manures. Unfortunately travellers have given us much too little information of the various ways in which agriculture is carried on in different lands. As plants that are cultivated without manure we may name the Maize, Rice, Sugar-cane, Plantain, Banana, Manioc, Yams, Coffee, &c.; as regions in which no organic manures are employed, and in which irrigation alone is employed in the culture of plants, we may mention Central Russia, in Spain the district of Malaga, Arabia, Hindostan, Binnan, Java, Ceylon, Malacca, Siam, Cochinchina, Tonquin, a part of Japan and China, Van Diemen's Land, a part of New Holland, Polynesia, Abyssinia, Egypt, Morocco, Cape of Good Hope, Madagascar, Madeira, Chili, Mexico, the Brazils, a part of Canada and of North America. In a word, the way in which the experience of agriculture has been employed for a theory of the nutrition of plants, reminds one very much of the contracted horizon of a small town, Philistine.

In accordance with these views, then, we maintain the right to reject, without inquiry, every theory of vegetable nutrition which does not put

forward the same as its basis, and especially all theories which set forth organic materials as a *principal* source of nourishment for plants.

Although the leading propositions, through the above development, may appear to be perfectly firmly established, yet we ought not to disdain any individual fact that would confirm or extend their basis. To this end the observation of smaller parts of the earth's surface may serve, which we may in some measure regard as a separated whole.

The Pampas* of Buenos Ayres, at the time of its discovery by the Spaniards, exhibited the same character as it does at the present day. Endless plains, with mostly a poor though, in the low-ground, a cheerful growth of grass, interrupted by paths, and here and there hedged in with strips of Algarobias and Acacias, present themselves, and besides the grave Bizcacho, the Turuturu, and similar small animals, are seen Ostriches, herds of Guanacos, and a scarce population of men. All these remain; but the Spaniards brought with them between 1530 and 1532 horses and horned cattle, which, getting wild, have increased in such immense numbers, that during the war of General Rosas with the Indians 20,000 horses were often lost in a few days. They wander about in countless herds, numbering about 15,000 in each, so that horses and cattle have but little value. The European has extended himself over these districts, and has introduced in the neighbourhood of the great cities a more luxurious vegetation, and the artichoke and the thistle occupy large portions of land. The organic substance in these regions, so far from decreasing, has apparently greatly increased. At the same time, the land, without receiving any remarkable contribution of organic matter since that time, has yielded, in constantly increasing proportions, immense quantities of organic substances.† The hides alone would represent an annual loss of 60,000,000 lbs. of organic substance. But this is only an inconsiderable part. According to their products, these herds cannot be estimated at much less than 20,000,000, and in a single year they would destroy by the process of nutrition 80,000,000,000 lbs. of organic matter, or in 100 years 8,000,000,000,000 lbs. All this organic substance must come from plants; and who could advocate the senseless position, that all these substances were once humus, or some other organic matter stuck in the barren soil of the Pampas?

A great part of Central Russia is covered with a soil, which, on account of its colour, is called by the Russians *Tschornoisem*, black earth, and is distinguished for its extraordinary fruitfulness. The rural economy in this district is about the roughest in the world; manuring is never once thought of; and those crops alone are sown which momentarily promise the greatest return for the least amount of labour. Berzelius has given an analysis of this soil by Herrmann, according to whom a more useful soil does not exist: —

| | | |
|---|---|---|
| Crenic acid<br>Apocrenic acid<br>Humic acid | combined with iron and alumina | = 5·66 per cent. |
| Humus extract | . . . . . | = 3·10 |
| Humin and roots | . . . . . | = 1·66 |
| | | 10·42 |

* Darwin, op. cit., and Tschichatschew's Reisen durch die Pampas.

† According to M'Culloch, in a period of five years, from 1838 to 1842, Monte Video and Buenos Ayres yielded annually about 90,000,000 lbs. of oxen and horses' hides, 9,500,000 lbs. of horsehair, and 3,250,000 lbs. of ox horns.

Let us suppose this would yield 6 per cent. of organic substance, which is the outside of the fact. The old Hessian acre (Morgen) (40,000 □ F.) bears, according to Block, at least 1710 lbs. of straw and 500 lbs. of grain. I will put it down at only 1076 lbs. of organic substance for the two. The depth of soil may be taken at 12 inches, the cubic foot 2·0 P. sp.; thus each Morgen, through cultivation, would yield 57,600 lbs., which, according to the above calculation, would suffice for a culture of 500 years. But mould, according to Saussure, loses, through putrefaction, at least 5 per cent., so that, according to the above calculation of its quantity (6 per cent.), in the first year it would lose 14,400 lbs., so that the 57,600 lbs. would not supply 10 years' consumption. This analysis of Herrmann must be allowed to be very bad. With the clay he finds no trace of alkali, although the soil had grown wheat for centuries, and no phosphoric acid, except 0·46 per cent. of phosphate of iron and alumina. A better analysis of this highly interesting soil is wanted. That these calculations, however, may, on the whole, be relied on is proved by other cases. The arable land of the Saalaue at Jena contains nearly one per cent. of humic acid combined with ammonia, and is a very beautiful wheat soil. The specific gravity is 2·59, so that the top soil, 12″ deep, of a single old Hessian Morgen of 40,000 □′ weighs 6,800,000 lbs., and consequently contains about 68,000 lbs. of humus. According to Boussingault, a soil in an average state of culture delivers 1050 lbs. per Morgen more organic matters than it receives through manures, so that these fields must be exhausted in 70 years, and, if the putrefaction is reckoned, in 25 years. But this arable land has been formed within the last century by the breaking up of meadow land, some of which still remains and is remarkable for its growth of grass; the average of six analyses of this meadow land gives 0·49 per cent. of humus, or about half of that of the arable land.

One of the most striking facts demanding an explanation of the defenders of the organic theory of vegetable nutrition is the agriculture of the Alps. No one thinks of manuring these alpine pastures; countless herds are nourished in the summer upon its grass and herbs, and return at the utmost in their excrements but half of the organic substance they take up. Large quantities of cheese are annually conveyed away from these pastures, with no return but thanks; hay is also taken from them and converted into dollars. This system has been carried on in the Alps for centuries, in some places for a thousand years, and yet no one has observed any deficiency in the fruitfulness of these regions. Can any one be so foolish as to maintain that the thin covering of soil which often lies upon the naked rocks is so rich in organic substances as to furnish this constant loss without exhibiting any remarkable change?

Lastly, we can make a calculation for the cultivation of land for an indefinite period. According to Boussingault, a Morgen of well-cultivated soil on an average yields 2480 lbs. of dry organic substance, and receives in manure only 795 lbs., or not more than a third part.* Every well-cultivated soil, instead of being the poorer in humus from the loss of organic substance and the attendant putrefaction, is the richer. It is not, however, necessary to refer to the investigations of Boussingault, as any one may be convinced of the absurdity of the humus-theorists by

* An objection might be urged here, that the ammonia is lost in the drying of the manure; but I have only taken into consideration the dry organic substance of the manure.

examining their own data for regarding the organic constituents of plants as a principal source of their nourishment.*

Boussingault has performed an interesting experiment on a small scale. He sowed 1·072 mgr. of peas in a mixture of burnt clay and sand, and watered it with distilled water; the ripe plants yielded 4·441 mgr., thus making 4·14 times as much as was sown. According to Block, when 138 lbs. are sown on an acre, in the third year of the manuring 880 lbs. are harvested. In burnt clay or sand the harvest would have been 571·32 lbs., according to the result of the experiment by Boussingault, the difference showing how much organic substance is necessary for the healthy development of the peas. The same experiment has been tried on a large scale, with far more splendid results, for many centuries in Cuba, and for 60 years in France. The *Tierra colorada*, in the higher regions of the island of Cuba, produce from year to year the richest harvests of Coffee and Indigo. This soil is never manured, and is a pure clay, which in other places would be called an iron soil. A very accurate analysis of this earth, in the Laboratory of the Agricultural Institute of Jena, by Herr Wapler, gave the following results: —

The earth is very fine, and contains only a small quantity of insoluble quartz, and small bits of chalk or limestone. It is soft to the feel, and of a dark brown colour.

| | | |
|---|---|---|
| *A.* Soluble in Hydrochloric acid . . . . | | 24·0 |
| Oxide of iron . . . | 12·20 | |
| Alumina . . . . | 6·00 | |
| Carbonate of lime . . | 5·80 | |
| Magnesia . . . . | traces | |
| | 24·00 | |
| *B.* Insoluble in Hydrochloric acid . . . . | | 75·4 |
| *a.* Humic acid, soluble in ammonia | traces | |
| *b.* In Sulphuric acid, soluble in potassa . . . . | 1·41 | |
| Alumina, with traces of oxide of iron . . . . | 34·34 | |
| Magnesia . . . . | 0·71 | |
| *c.* Silica . . . . | 38·94 | |
| | 75·4 | |
| *C.* Loss . . . . . | | 0·6 |
| | | 100·00 |

In France the following experiments have been made between the mouths of the Gironde and the Adour. The sand-downs which are washed from the sea are carried by the west wind into the interior, and thus large districts of the land are converted into a kind of

* Thus, according to the calculations of Block (Mittheilungen landwirthschaftliche Erfahrungen und Grundsätze, vols. i. and iii.), a good wheat soil will yield annually 2075 lbs. per acre of dry matter, and receives 1167 lbs. of dry manure; but the manure contains, on an average, 30 per cent. of ashes, whilst the cultivated plants contain but 5 per cent., so that the proportions of organic substances are as 794 to 1971.

Sahara. After many purposeless attempts to arrest the movement of this sand, by planting wood, the sound plan was hit upon in the year 1789, of planting these sand-hills with coniferous trees. This perfectly succeeded, and in the year 1809 there were already 15,000 Hessian acres converted into a pine forest, which had grown upon the driest possible soil, and which was entirely destitute of organic substance. The same phenomenon is seen in the pine forests of the Mark and in the oases of the Sahara. In most cases where the inorganic elements of the soil are suitable, and water is found in sufficient quantities, vegetation is possible upon the surface of the earth.

Lastly, I will refer to a point which unfortunately I cannot illustrate with figures, as no accurate data exist. Our economical arrangements generally, and the way in which rain water is necessarily got rid of from our cultivated soils, and carries with it into brooks and streams their soluble constituents, make it certain that all our rivers carry annually to the sea a large quantity of organic substance from the land. If we were to calculate this loss for the more considerable rivers, according to the quantity of organic matter their waters presented on chemical analysis, it would probably greatly exceed all our conceptions. As instances, I would refer not merely to the organic substances, but to the entire plants and animals, which are annually brought down to the sea by the two great rivers of America, the Amazons and the Mississippi.

In short, regard this matter as we will, the theory which would derive the food of plants from the organic substance of the soil is a remarkable example of the perversities to which a hypothetical natural history may lead without fundamental principles. To show how thoughtlessly the humus-theorists have gone to work, a single example will serve. According to Sprengel, plants derive the principal part of their carbon from humic acid. This they take up as humate of lime, and the advantage of lime to the soil is supposed to lie in its forming this salt with humic acid. It contains, according to Sprengel, 1 lb. of lime and 10·9 lbs. of humic acid. But the produce of wheat on an acre (after four years' manuring, according to Block) in straw and grain would be 1071·24 lbs. of carbon, which would require 1552·52 lbs. of humic acid, which would require 142·43 lbs. of lime to convert it into humate of lime. But this wheat contains, at the highest, in the grain 0·527 lbs., and in the straw 8·873 lbs. of lime, which is about $\frac{1}{15}$th of what it ought to contain. And if we take, for example, the clover, which, for this view, is the most advantageous of plants, we shall find the result the same. According to Block, an acre of clover contains 1020·73 lbs. of carbon, which is equal to 1479·32 lbs. of humic acid, which would require 135·7 lbs. of lime in the plant, whilst in, reality, the clover contains only 40·29 lbs., or about one-third the quantity.*

§ 191. The organic substance of vegetables, so far as the

* Through the absence of the necessary bases alone, the impossibility of the nutrition of plants through humic acid is proved. At the same time, Liebig's attempt to disprove the theory, on account of the insolubility of the humates, must be regarded as a failure. The rain which falls upon the earth supplies only the smallest quantity of moisture which is taken up by the plant. Dew, and especially the absorption of vapour through clay, humus, &c., affords a much larger quantity. It does not appear probable that water would fail. An acre of 40,000 □ feet of meadow land vaporises, according to Schübler, in 120 days, 6,000,000 lb. of water, which is twelve times as much as falls, on an average, in Germany (Tübingen) as rain-water in an equal period of time.

question of their nourishment is involved, may be divided into two classes, one containing no nitrogen, and the other containing this element. The first class may be divided into three groups: one in which, together with carbon, hydrogen and oxygen are found in the proportion requisite to the formation of water (dextrine, &c.); a second, in which oxygen is present in superfluity (vegetable acids); and a third, in which it is found in very small proportions, or in which it is altogether absent (the oils). The second class (the protein compounds) contains, together with the four organic elements, sulphur and phosphorus. Hydrogen and oxygen are always present in sufficient quantity in plants in the form of water, without which no vegetation is possible. Carbon is furnished from the carbonic acid derived from the processes of burning and respiration, from putrefaction and from volcanic eruptions; all of which render it to the atmosphere from which it is received by the vegetable world. Nitrogen is taken up in the form of ammonia, or the salts of ammonia, which are found during the commencement of the processes of combustion, respiration, putrefaction, and during the eruptions of volcanoes. Suphur and phosphorus are yielded probably from phosphuretted and sulphuretted hydrogens. The last is formed whenever protein compounds containing sulphur putrify, and whenever organic matter is decomposed in contact with the sulphates, and also during volcanic action.

In the foregoing paragraphs, I have shown how plants over the whole earth, in order to obtain their food, need the mediation of the inorganic world; for through it alone organic substances minister to their existence, for plants cannot receive their nourishment in the form of organised, but in the form of unorganised matter. In this place we must afford especial proof that the individual elements are taken up in the inorganic, and not the organic, form, and also point out the essential sources of these combinations. I may, for the time, lay aside any discussion respecting the absorption of hydrogen and oxygen, for no plant can vegetate without water; and usually much more water is received into the substance of a plant than is requisite as the mere vehicle of hydrogen and oxygen. But I must notice sulphur and phosphorus, on account of their union with protein to produce albumen, fibrine, and casein. All the observations which have already been made on organic substances in general will apply to carbon and nitrogen: there is, however, much of a special nature, and in relation to carbon some interesting facts to be brought forward; whilst, with regard to nitrogen, and especially on the sources of ammonia, much has yet to be added.

1. *Carbon.* — Over the whole face of the earth, with the exception perhaps of some few savage tribes little known to us, man is acquainted with the use of fire in the preparation of his food, and in the colder zones for the purpose of communicating warmth; whilst in the torrid zones it is used also to keep off wild beasts and deleterious insects. Civilised nations employ it also for a variety of purposes in the arts. Amongst the civilised nations of the temperate zones, combustible materials are used indeed with economy, and especially in cases where numbers live together in one house, since the fire which will warm one

individual will warm, at the same time, several; and for culinary purposes, the fuel requisite to cook food for six men at one time is less than would be required to cook six several meals for one man. Where there is no limitation in the production of fuel, large quantities are needlessly consumed. A great proportion of the inhabitants of the tropics* live upon rice, which must be long under dressing by fire before it is eaten. Extensive conflagrations of forests are even yet frequent; in America, they continually occur when new land is taken into cultivation. Taking together all these facts, I believe that we may arrive at something like an average yearly consumption of fuel to each man, by estimating the quantity consumed between 50° and 60° N. lat. According to the calculation made of the consumption of fuel in the barracks at Weimar, in some institutions for boys, in some hospitals, and in sundry families of large size, I reckon that a medium quantity of fuel consumed for each head annually amounts to one klafter of hard wood. A klafter of hard wood weighs on an average 3600 lbs., and contains about 50 per cent. of carbon. So that a thousand million of men, for domestic combustion, would consume 1,800,000,000,000 lbs. of carbon.

For use in the arts and manufactures, I calculate on the use of coal. In England, indeed, coal is consumed for household uses; but then elsewhere wood, turf, and brown-coal are sometimes used in the arts and manufactures. According to Karmarsch and Heeren, the coal obtained yearly in England, France, Belgium, Prussia, Austria, Saxony, and some of the smaller German states, amounts to 75,000,000,000 lbs. The countries not enumerated (and especially North America) in the calculation would probably make it amount to about 80,000,000,000 lbs. If this contained 72 per cent. of carbon, it would give an average of 60,000,000,000 lbs. carbon, which would give 200,000,000,000 lbs. of carbonic acid. In addition to this, the process of respiration yields about $2\frac{1}{2}$ billions lbs. of carbonic acid. Household fires may be computed to give $6\frac{1}{2}$ billions. The processes of putrefaction and fermentation may be estimated as follows. To every square rood we may allow at the least 100 lbs. (something more than 0·5 per cent.) of putrifying animal substance, of which yearly 2 lbs. of carbon is converted into carbonic acid by decomposition. This we assume as an average result drawn from De Saussure's direct experiments. After the subtraction of the desert of Sahara, and other large deserts, and of the polar regions, where vegetation is impossible, the solid land remaining amounts to 3,000,000 square miles; so for the processes of decomposition 90 billions lbs. of carbonic acid are obtained. Exclusively of volcanic operations, the carbonic acid generated in one year amounts to 100 billions lbs., or in 100 years almost ten times as much as is present in our atmosphere; and 500 years would suffice to make the air irrespirable for men and beasts, if there were not a provision in the economy of nature for subtracting the carbonic acid again from the atmosphere, which should be continually carried on. Such provision is found only in the vegetable world.

The carbon produced in the processes of breathing, putrefaction, and, for the most part, combustion, is annually afforded by the vegetable world, and being freed from its union with organic matter, is converted into inorganic carbonic acid. Can any reasonable man believe that the store of organic substance upon the earth could long withstand such

* When we reflect on the dense population of China and India, we may perhaps assume that a third part of the inhabitants of the globe live on rice.

constant loss? The carbon consumed by breathing yearly alone corresponds to the full produce of 500,000,000 acres of the finest wheat-land, or a surface more than twice as large as France.*

Whatever may have been the manner of the first production of plants, few will be inclined to assume that the mountains, when they first rose from the sea, were thickly covered with humus. It is much more probable that they were at first quite naked, and that they were but very gradually covered with mould by means of vegetation.

Upon this earth, at first void of humus, the vegetation of the coal formation was first developed, the extent of whose remains still fill us with amazement. Should the store suffice to cover the present demand for yet 2000 years to come, as some English geologists† have assured us that it will, then these mineral coals, assuming that in decomposition their loss would only be 20 per cent. of carbon, would have a weight of 1290 billion lbs. of carbon, which manifestly could not be derived from the original earth void of humus.

If we consider now the cultivation of individual plants, we find such data as follows:—The sugar-cane requires a good damp soil, but which is never manured. The acre produces about 4700 lbs. of cane, which contains at a minimum 700 lbs. of carbon in sugar, 500 lbs. of carbon in the pressed cane; the sugar is taken away and the cane is burned in the sugar-making houses; 1200 lbs. of carbon are thus yearly drawn from the earth without any return (Boussingault). The soil in the French colonies, used in the culture of sugar, must in this way yield yearly 225 million lbs. of carbon, which would correspond to a loss of 325 million lbs. of humus.‡ We may reckon, on the whole, that the tropical regions produce, from coffee and sugar alone, annually about 2300 mil-

* The produce of the acre amounts, according to Block, to 475 lbs. of grain, and 2970 lbs. of straw. The quantity of the carbon of the grain amounts to 46 per cent., and of the straw to 48 per cent., according to Boussingault.

† Mr. Taylor, one of the most extensive proprietors of coal mines in England, reckons that the store of coals in Durham and Northumberland alone would suffice for the consumption of these provinces for 2,500 years yet to come; or, in case of falling off, at least for 1700 years. Bakewell, in his Geology, reckons that the coal-beds of South Wales alone would suffice for the present necessities of all England for nearly 5000 years. Both these reckonings are accepted by distinguished geologists, and only objected to by some practical men, in so far as they conceive that too little allowance has been made for loss in working, an objection which does not affect our present case. According to the statements of Lindley and Hutton, in the "British Fossil Flora," the coal-beds of the State of Ohio, covering an extent of 12,000 square miles, calculated at an average thickness of five feet, would give a quantity of carbon amounting to 70,000,000,000,000 lbs. We cannot estimate with great exactness the contents of the various coal-beds upon the earth; but when Liebig supposes that the carbonic acid now present in the atmosphere contains by far more carbon than all the coal-beds in existence, he manifestly errs greatly. The carbon contained in the carbonic acid of the atmosphere certainly cannot amount to a tenth part of that contained in the whole of the coal-beds upon the globe; and we do not assuredly over-estimate the loss during decomposition and putrefaction, if we rate it at a twentieth part of the carbon which this past vegetation contained during life.

‡ The sugar-cane contains on an average—

| | |
|---|---|
| Of dry Vegetable fibre . . . | 11·0 |
| Sugar . . . . . | 15·5 |
| Water . . . . . | 73·5 |

In the pressing, 8 per cent. of sugar is the maximum obtained; thus 8 lbs. of prepared sugar, and 26·5 lbs. of dry organic substance, corresponds with 40 per cent. of carbon. The French colonies produce yearly 80 mill. kilogr. The islands of Bourbon and Mauritius yield annually about 100 mill. lbs., and thus lose yearly about 130 mill. lbs. of carbon.

lions of lbs. of carbon, which, partly by the process of burning, and partly by that of respiration, produce at least half that quantity of carbonic acid.*

The Oil-palms (*Cocos nucifera* and *Elais guineensis*) grow in sea-sand. The culture of the latter is largely carried on on the West coast of Africa, in moist damp sand, not enriched by manure. Between the years 1821—1830, England alone imported from the coast of Guinea 107,118,000 lbs. of palm oil, and therewith about 76 million lbs. of carbon, drawn from a soil which in itself contained no carbon. At present the yearly import is about 33 million lbs. of oil; so that the soil upon which the palms grow must, in order to supply the yearly export of oil, deliver about 25 million lbs. of carbon.

The banana, however, affords the most striking example of the production of carbon. It is usual to plant it originally as a slip, upon a moist rich soil, without any manure whatever; from the time it becomes capable of bearing, it is allowed to produce for twenty years before any new trees are planted, and when at last new shoots are put in, it is not because the old trees cease to bear, but because the plantation is become confused and disorderly, owing to the continual dying away of the old shoots, and the pushing up of new young shoots from the old roots. According to Humboldt, an acre produces about 98,808 lbs. yearly, which corresponds with about 43,245 lbs. of dry substance, and at least 17,000 lbs. of carbon; hence in twenty years such a surface will yield the prodigious quantity of 345,960 lbs. of carbon. By this, however, the soil is by no means exhausted. The culture has probably been carried on uninterruptedly for a thousand years in the South Sea islands. On the contrary, the soil is constantly rich in humus, and rendered yet more fertile by the continual shedding of the leaves, and the quick process of putrefaction in those regions.

It is known how large are the crops of rice produced from the soil on which this vegetable has been long in constant cultivation, and yet that soil is for the most part never enriched with manure, but only watered. According to Darwin, the richest maize harvests are obtained from the interior of Chili and Peru, from the most sterile quicksands, which are never enriched by manure, and where only small streamlets from the Andes supply any water. There are great expanses of sand, which within the last half century have gradually become covered with birches and firs, and which yet discover spots of the original barren quicksand. So far as my information extends, there is no part of the earth where the inhabitants have applied manure to assist the growth of forests. Yet each forest annually yields to us a considerable quantity of carbon in wood, which is converted into carbonic acid by the process of burning. And it is a fact, long known, that the soil of forests becomes annually not impoverished, but, on the contrary, enriched by the decay of its own leaves, and thus has a large amount of the ingredients requisite to the support of vegetation. As an example of this, we may mention the en-

* The total production of coffee is about 480 mill. lbs.; of sugar, 1600—1700 mill. lbs. The carbon is generally reckoned only at 40 per cent. 1650 mill. lbs. of sugar give 660 mill. lbs. carbon, half of which is converted into carbonic acid; 3816 mill. lbs. of cane contain 1126 mill. lbs. of carbon, which is burnt; the coffee contains 192 mill. lbs. of carbon; so that coffee and sugar together throw into the atmosphere annually about 6043 mill. lbs. of carbonic acid gas. During nutrition the non-nitrogenous compounds are entirely, and the nitrogenous are partly, converted into carbonic acid gas.

tire district of Brandenburg, whose soil consists entirely of sea and down-sand. It is still in many places composed of a loose and pure quick-sand of 100 feet deep, and so moveable that it does not, as I have had an opportunity of witnessing in the neighbourhood of Berlin, require any very high wind to change entirely the configuration of the surface. Such spots are found likewise between Charlottenburg and Grunewald, and between Berlin and Tegel. Young pines are sometimes found standing with their first branches buried in the soil, and after eight days with a naked stem, three feet in length, and the roots so exposed that one could creep through them. This soil, as is seen in the Spreewald, so far as it is moistened by the rivers Spree and Havel, produces vigorous pine vegetation, which most certainly cannot draw all its carbon from sources furnished by the soil, for it has never possessed it, nor has it been furnished to it by artificial processes. The older standing forests have obtained by the fall of the leaf and the action of wind upon the trees so much organic substance as to become in a measure suited for arable land, though such land yield very poor crops of corn, because it needs the essential physical and chemical qualities, which only can be supplied by active culture, and the addition of the salts required by the *Cerealia*.

In the cases adduced, we find a production of carbon in organic compounds which clearly could not arise from the elements of the soil, because it either contained none originally, or would soon become exhausted of that which it contained; and yet it becomes continually richer in carbon, even though the decay of vegetation continually carries it off, and with astonishing rapidity under the tropics. The substance of the soil, then, is assuredly not the source from whence plants derive their carbon, and no other is left but carbonic acid. Hence it can be easily understood that the carbonic acid of the soil may contribute to the food of plants, as well as carbonic acid derived from any other source.

It becomes a question whether there is enough carbonic acid existing to supply the necessities of vegetation upon the whole earth.

Supposing the part of the earth which is covered with vegetation to be one-fifth of the entire surface, that will give a space of two millions of square miles, or of 43,124 millions of acres; upon each acre we may allow an annual produce of 2000 lbs. of carbon, which, on an average, is certainly not too little; we have to provide for a yearly demand of about 300 billion lbs. of carbonic acid, the source of at least a third part of which we have seen above. How near this is to the truth, we may ascertain by considering some secondary facts. North America alone produces (according to the North American Almanac for 1843) annually 219,163,319 lbs. of tobacco, which being burned, would yield about 340 million lbs. of carbonic acid, so that the yearly produce of carbonic acid from tobacco smoking alone cannot be estimated at less than 1000 million lbs. Other very extensive processes involving the formation of carbonic acid are not alluded to in the above computations. Calculations have been made respecting the disengagement of this gas from the lungs; but from the want of data none have been made upon the production of it from the skin, which is no less important. In the same way, many processes of combustion, which are carried on in various methods of culture or in other cases, are entirely overlooked in our calculations. In the whole of Northern Germany, the burning of moors is a very common practice; below Ems it is annually done on the largest scale. So in Corsica, the *makis*, or evergreen shrubs, are cut down once in three years, and burned upon the soil. In North and South America the breaking up of new

land always commences with the burning of the aboriginal wood, which is occasionally done also in the Old World, especially in Russia. Amongst the various burnings is also that of the Steppes, so frequent in the Pampas and the prairies of North and South America. Exceeding all these, are those incalculable quantities of carbonic acid which continually issue from volcanoes. When all these sources of supply are put together, we can entertain no doubt that the carbonic acid annually produced upon the surface of the earth is abundantly sufficient to supply all the demands of vegetation.

The foregoing will serve to make clear the relation of plants to carbon, and the great part which carbonic acid plays, and must play, in the economy of nature.

2. *Nitrogen.* — The views of botanists upon the taking up of nitrogen by plants are in a twofold manner opposed to those upon the appropriation of carbon. It is eighty years since the discovery of oxygen and its qualities by Priestley showed the immense importance of carbonic acid to the vegetable world; but there is still at the present day a great number of botanists, and theoretical agriculturists, and even some chemists, who entertain the conviction that the organic matter of the soil is received by plants in order to supply them with carbon. Again, it has been recently ascertained that ammonia, and the salts of ammonia, are the only essential sources of the nitrogenous contents of plants, although there may yet be found persons ignorant enough to believe that plants receive their nitrogen from the soil, and who overlook its change in manures into ammonia and the salts of ammonia. The fact is, it is simply impossible to oppose any thing to ammonia and its salts as humus has been to carbonic acid. We are unacquainted with any soluble organic substance containing nitrogen, which is present in the earth in sufficient quantity to supply the necessities of plants, and all experiments have led to the result that neither animals nor plants are capable of assimilating nitrogen in its elementary form. There is nothing left to the theorists on organic nutrition and vital powers but to receive it in the form of ammonia. The simple question to be solved here is, What are the sources of ammonia? and in the discussion of this question it will be requisite to distinguish between cultivated plants and those growing wild.

It hardly needs to be observed, that plants growing wild are not supplied with ammonia through manuring or other organic supplies; nor can they be, according to De Saussure, who was the first to point out this fact, that the atmosphere is the source from whence plants derive their volatile salts of ammonia, and which have been supplied from the soil. A second source has been recently pointed out by Mulder, namely, the formation of ammonia at the cost of the atmospheric nitrogen by the putrefaction of non-azotised organic substances.* We can make no accurate computation of the amount obtained in either way. We know that the last result of the putrefaction and decomposition of substances

* Mulder, moreover, regards as important, in which I agree with him, the gradual formation of ammonia in the soil. I attach little value to the objection to De Saussure's experiments, that in the decomposition of the non-azotised compounds, which for the most part contain oxygen and hydrogen in the proportions to form water, there is no free oxygen, which ought to be the case if the hydrogen combines with the nitrogen to form ammonia. But it is highly probable that the sources of nourishment are universally the same for all plants, and that this formation of ammonia, according to Mulder, may occur on every primitive soil. and yet leave no organic matters.

containing nitrogen consists in the separation of the nitrogen in the form of ammonia; thus alone, each perishing generation would produce enough nitrogen to furnish the next generation with an equal amount. It is first given to the atmosphere in the form of ammonia, from which it is received by plants in order to be again introduced into the circle of organic existence. We know also from the researches of Daubeny and Jones that ammonia is one among those gases which issue in large quantities from volcanic strata.* By this means large additions are made to the stores of ammonia obtained from its sources. As yet no experiments have been made respecting the amount of ammonia contained in the air, but it is known to vary much more with locality and at different times than does carbonic acid. Those who have had any experience in chemical labours, know how very difficult it is to exclude ammonia, which penetrates every where. Every bottle of hydrochloric acid that is not very tightly secured, every bottle of sulphuric acid that has not been perfectly cleaned, affords, in a crust of ammonial salts which forms upon it, the proof of this. All water, especially rain water, and still more snow, contains ammonia.

The most striking example of the production of nitrogen without the same having been first furnished in the form of manure, is found in irrigated meadows (Rieselwiesen), which annually yield from forty to fifty lbs. of nitrogen in organic compounds †, whilst on an average the produce of manured land yields only thirty-one lbs., and after subtracting that which was contained in the manure, only seventeen lbs. As we have already seen, plants cannot draw this nourishment from the organic elements of the soil, and this is especially the case with nitrogen. This is seen in mountain districts and meadow lands which are employed only for the breeding and rearing of cattle, and which yet allow more nitrogen to be carried from them than is obtained by any other mode of tillage. It is also confirmed by the amount of nitrogen contained in plants being wholly independent of the amount of the nitrogen supplied by manure.

In the south, and more especially in the central parts of Russia, the agriculture carried on by the peasantry is of the lowest kind. Manure, where used at all, is exclusively confined to garden and flax tillage; the fields are never manured. Hence their produce is only from five to six fold.‡ Yet each acre yields in the harvest 14½ lbs. of nitrogen; and in Central Russia, where we may suppose the land to have been in cultivation for 1000 years, each acre must have yielded, without any compensation, 14,500 lbs. of that substance.§ The export of corn from Odessa in the year 1827 contained not less than 755 million lbs. of nitrogen.‖

* The Ammoniacal Grotto near Naples (Gazette Medicale de Paris, No. 49. Froriep's Notizen: 28, 257.).

† Irrigated meadows (Rieselwiesen), according to the German farmers, Linke, Schwerz, &c., yield from 30 to 40 centners of hay. Dried hay, according to Boussingault, contains 1·29 per cent. of nitrogen.

‡ This poverty of crop is not universal. In some districts of the Ukraine no manure is used. The straw is burned. The corn grows so vigorously that the stalks are as thick as that of the reed, and the leaves resemble those of maize; whilst crop after crop is drawn from the same soil, with only one ploughing between the harvest and the sowing. (Loudon.)

§ The sowing of 1½ Berlin bushels of corn yield six bushels at harvest, or 540 lbs. The produce of corn to straw is as one to two, making 1080 lbs. of straw. Wheat dried at 110° Cent. yields, according to Boussingault, 85·5 per cent. of dry material, and thus 2·3 per cent. of nitrogen; the wheat straw 74 per cent. of dry matter, and in that 0·4 per cent. of nitrogen.

‖ Odessa exported in the year 1827 1,200,826 Tschetwert of wheat, 39,940 Tschet-

From this we are naturally led to a closer observation of cultivated plants. I have already shown that irrigated meadows which are not manured yield yearly a much larger amount of nitrogen than lands under tillage. Hence it appears improbable that cultivated plants should require nitrogen from the manure which is supplied to them, since the same sources from which wild plants receive that element are open to them also. I believe that it is more than probable that plants under culture are as entirely independent of manure, so far as it contains nitrogen, as wild plants themselves. The experiments of Boussingault, against which no objection can be made, seem to prove this. Boussingault is an experienced practical agriculturist, a distinguished naturalist, and a superior chemist. The great number of his experiments, and their extreme simplicity, leave no room for objections. Boussingault cultivated the plants which he observed in the usual method, and made most accurate investigations as to measure and weight; and these he places before us instead of guesses or fancies. The results which he obtained as to the weight of produce, the quantities of manure, &c., agree in the main with those of experienced German agriculturists, and exhibit a medium between their extremes. An objection which has been put forward by Liebig, that the nitrogenous matters of the manure evaporate during the process of drying (at 110° C.), might have had some weight, had he established the fact by experiment. The ammonia of manure is either disengaged and volatile, or it is not volatile at 110° C. In the last case the objection is at once answered, and I believe this to be the fact with the generality of the ammoniacal salts contained in manure; but in the first case, that portion of the salts of ammonia which is volatile is not directly taken up by plants, but is dispersed in the air by the ploughing and turning about of the soil. The manure is not immediately or continually supplied to each plant commencing vegetation; it is put into the ground, often some time before the seed, turned about as the soil is turned, and thus most probably its action extends over the four, five, or six years consumed by a rotation of crops. It must be at once seen that by the second or third year the earth will hardly contain any remnant of the ammonia salts supplied to it with the manure. Now the independence of the nitrogen in plants of what they receive from manure, is proved by the fact that the amount produced is not larger the first year, and then gradually decreasing, or the contrary; but it depends rather

wert of rye, and 6,852 of barley; in the whole, about 40,000 million lbs. of dry organic substance, which was more or less directly produced from the soil: and it would be impossible to allow that more than 1,000,000 lbs. of dry organic substance could have reached the soil in the form of manure. A similar calculation may be made for St. Petersburg. What needs to be done is the laying a basis for a new science, which, by means of most accurate measurements, weights, and analyses, shall supply commercial statistics, and the elements of a national economy, in those forms of matter which constitute the food of plants and animals. We cannot tell how important might be the result, for the benefit of mankind, if we could once be placed in circumstances that should enable us to subject to calculation, and thence also to control, the escape and influx of the elementary substances, their interchange between sea and land, and between both and the atmosphere. Happy would be the country, and sure to carry agriculture to the greatest perfection, which should learn the means of regulating the quantity of the organic elements (carbon, hydrogen, oxygen, nitrogen) in proportion to its area, - which should possess the art to draw upon the inorganic stores of the atmosphere, and thereby to spare all waste, and multiply the means of fertilising the earth — to export its superfluity of some elements, and to import those of which larger supplies would be beneficial.

upon the nature of the cultivated plant. In a six years' rotation of crops, was yielded in

| | | | Nitrogen. |
|---|---|---|---|
| 1st year | by | Potatoes, on the acre | 24·75 lbs. |
| 2nd | „ | Wheat . . . | 18·92 |
| 3rd | „ | Clover . . . | 45·21 |
| 4th | „ | Wheat and Turnips | 29·93 |
| 5th | „ | Pease . . . | 52·63 |
| 6th | „ | Rye . . . | 17·33 |

In the whole, 188·77 lbs. nitrogen were produced, whilst the manure spread at the beginning contained only 130·31 lbs. of nitrogen. Again, in three rotations of crops, two of five years, and one of six, an equal quantity of manure was supplied to all; namely, for the year and for the acre 21·90 lbs.; but the annual superabundance of the nitrogen obtained over that contained in the manure was, in

| | | | |
|---|---|---|---|
| 1st course of | 5 years | | 5·06 lbs. |
| 2nd „ | „ | | 5·45 |
| 3rd „ | 6 | „ | 9·83 |

This last fact is sufficient of itself to show the independence of the production of nitrogen of the contents supplied in manure.

In six rotations, embracing twenty-one years, the average produce of nitrogen from all the harvests, as compared with the manure supplied, was as 1 : 2·8. According to information afforded by Crud in the culture of Lucerne, Boussingault reckons it as 1 : 4·8. It is supposed that a positive proof of this dependance of the production of nitrogen upon the quantity conveyed to the plants in manure, is found in the fact, that with the increase of the one there is an increase of the other. But it is obviously an error to confound what may be a coincidence with cause and effect. If the fact was as represented, why does a plant always sink to the ground when watered with a solution of ammoniacal salts? Manifestly because the healthy and strong development of the plant, and therewith the assimilation of the nitrogen, demand further conditions than simply the presence of salts of ammonia. I would here also direct attention to the close connection between the salts of phosphoric acid and the nitrogenous substances of plants. Liebig has correctly stated that we must recognise the fact that the latter are never formed without the presence of the former; but he has not made experiments with various manures containing different proportions of nitrogenous substances and phosphates. It is possible that the nitrogen of cultivated plants may come from this source, and thus we may account for its quantity in them being constantly the same. Such plants find abundance of nitrogen at their command without need of receiving any through the medium of manure, for we see that with all applications of this kind we cannot produce so much as is yielded by irrigated meadows which are entirely unmanured.

We want much some exact experiments upon this subject. We can only adduce those of Schattenmann and of Kuhlmann: the first give almost a doubling of the produce of meadows after the application of carbonate of ammonia (Boussingault*); whilst those of Kuhlman† show the in-

* The favourable action of the salts of ammonia may perhaps be explained, according to the experiments of Schultze of Eldena, through some change produced in the mechanical condition of the soil.

† See Appendix A.

dependence of the produce of nitrogenous compounds of the manure. The production increases as fixed alkalies and organic salts are present, and still more as the salts of phosphoric acid are brought into action.

From the preceding we learn, that wild plants produce these nitrogenous compounds independently of the organic nitrogenous matters held in the soil, and of all forms of ammonia not proceeding from the atmosphere*; and this makes it at least in the highest degree probable that the same law holds good for cultivated plants.

3. *Phosphorus and Sulphur.*—The phosphorus and sulphur held in combination with the elements containing nitrogen are very insignificant. If we reckon all nitrogen as albumen, and take the highest produce of nitrogen which occurs, as in peas, we obtain about 2 lbs. of sulphur and 1 lb. of phosphorus as the produce of each acre of land in the year; that is, the soil, taken at 12 inches deep, must produce in the course of the year, in 434 lbs. of earth, one grain of sulphur and half a grain of phosphorus. Every 434 lbs. of earth corresponds to a surface of almost three square feet. Now, supposing that this phosphorus and sulphur arises from sulphuretted and phosphuretted hydrogen, whereby the improbable hypothesis of the decomposition of sulphates and phosphates is avoided, then we must assume that the earth, during a period of vegetation of 120 days, absorbs within twenty-four hours from an air-pillar of three square feet of surface of the soil, 0·0088 grains of sulphuretted hydrogen, and 0·0046 of phosphuretted hydrogen.† Now, if we take only 3000 cubic feet of air as entering into the calculation, then the cubic foot of air would need to contain only $\frac{1}{300000}$th of a grain of sulphuretted hydrogen, and $\frac{1}{600000}$th of a grain of phosphuretted hydrogen, in order to suffice to the total demands of vegetation. No person will attempt to prove the absence of this quantity in the air, and the possibility of its existence arises from the many processes of putrefaction, by which phosphuretted and sulphuretted hydrogen is delivered; and to these must be added volcanic processes, such as sulphureous springs, which give out quantities of sulphuretted hydrogen, and probably also of phosphuretted hydrogen, into the air. However, we may well lay aside the consideration of these minimal quantities, since questions of more importance demand our attention.

§ 192. The vegetable world in general receives its organic elements through carbonic acid, salts of ammonia, and water; this is probably sufficient for all the tribes of plants excepting the true parasites. Yet we cannot maintain that plants growing in a moor soil may not also need organic nourishment. Nutrition through inorganic compounds serves only for plants with roots, and in these only for the root-cells; all other cells — those which exist in branches, buds, and embryos, in connection with the mother plant, — are nourished exclusively upon matters already more or less assimilated.

* Whether this exists already in the atmosphere, or has been produced by the process of decay in contact with nitrogen.

† Peas, which of all cultivated plants contain the largest quantity of nitrogenous matters, yield somewhat more than 50 lbs. of nitrogen on an acre. In albumen, according to Mulder, there are 15·83 of nitrogen, 0·68 of sulphur, and 0·33 of phosphorus. If we take the most exorbitant case, that of Lucerne, we should have at the utmost in a cubic foot, the $\frac{1}{100000}$th of a grain of sulphuretted hydrogen, and $\frac{1}{200000}$th of a grain of phosphuretted hydrogen.

We should do very wrong and depart from our fundamental principles if we were from the foregoing considerations to deduce a theory of vegetable nutrition, and were to apply it to explain the mode of nourishment of particular plants. In order to obtain a correct theory of the nutrition of plants, we must first learn to know the plant in its other relations, and in this place the fundamental principle of the independent existence of the life of the cells must be taken into consideration. Every cell lives for itself. What is necessary for one cell is not to those around. One cell may stand in direct relation with inorganic nature; another, through its extensive union with other cells, may stand in an indirect relation between the plant and nature; it may receive its nourishment not immediately from the common sources of nourishment, but already assimilated and modified through the agency of other cells. Both conditions may occur to the same cell during different periods of its life: thus live the generality of the cells throughout the body of the plant: branches, leaves, flowers, and even parasites themselves, live only, or almost only, on matter already assimilated. Each bud, each twig, is a new individual, which sucks from the mother plant matter already become organic, and which appears incapable of assimilating inorganic matter. At this point it must first form root-cells, by which means it is placed in circumstances to receive and assimilate and convert inorganic matters into organic combinations. But even these root-cells possess only for a short time the capability of assimilating inorganic substances for the use of the plant. The older root-cells receive from those of more recent origin matter already assimilated.

A question which has been referred to in the foregoing paragraphs awaits an experimental solution. It may be thus expressed:

Are there truly, as Unger and Endlicher have asserted, hysterophytes; and if so, how many groups of plants belong to them, and in what way is their independence of a preceding vegetation demonstrated? There can be no doubt that parasites are hysterophytes, that is, that they can by no possibility originate until the subject on which they root themselves is formed. This may be asserted with respect to a large number of fungi, which are only developed on soil formed from the decay of former organisms. The difficulty of the cultivation of turf-moor plants on other soil than their own, seems to arise from a similar relation. The nutrition of the true parasites, from the assimilated juices of the subjects on which they appear, seems to be established. From these to the *Algæ* and *Lemnaceæ* there is a continuous series of transitionary forms: they can vegetate perfectly where water, carbonic acid, and ammonia are present; and it could only be presumptuous ignorance which should at present decide whether some of the remaining plants may not derive nourishment, in part or entirely, from organic matters. From what has been already said, it is at least clear that, with respect to cultivated plants and those on which available observations have been made, the organic substance of the soil is not to be regarded as the principal source from whence they derive their nourishment, because its amount is not adequate to the necessities of plants.

With respect, however, to the turf-moor plants, experiment alone can decide whether their nourishment, demanding, as it does, much carbon, is not essentially received from organic substance as such; for we know that on moors organic substance is present in large quantities in a dissolved state, and we have as yet no proof that the plants do not receive all which is presented to them in a dissolved form.

In all future experiments, it will be most important to bear in mind that each cell carries on its own existence, and that, therefore, what holds good for one cell does not necessarily apply to others. No cells, with the exception of some root-cells, feed upon absolutely raw material, as it is received from the earth; they live upon matter more or less assimilated, upon fluids that contain albumen (or the like), dextrin, grape sugar, and organic acids, but in which gum is probably never present, and cane sugar only in rare cases. Every individual which, as branch, bud, or embryo, still stands in connection with the mother plant when separated from the original plant, cannot continue to live on organic matter, and perishes unless it can appropriate inorganic matter by the formation of root-cells. All conclusions founded upon leaves, or other parts of the plant which have been separated from its entire body, are inadmissible as applied to the entire plant.

§ 193. For the perfect nutrition of plants, not only is the absorption of the organic elements and the sulphur and phosphorus found in combination with the nitrogenous substances requisite, but also the inorganic salts which they contain. All plants that have hitherto been burned, with the exception of the mother of vinegar, have been found to leave behind them an ash, which must have been taken up by the plant. These substances must be regarded as essential to the nourishment of plants, though as yet we do not understand in what consists their importance. We may, with Liebig, arrange plants or their organs into four classes, according to the predominating elements left in the ashes (when above 50 per cent.):

Alkaline plants: succulent, containing meal and sugar.
Chalk plants; Dicotyledons, leaves, fruits, and stalks.
Siliceous plants: Monocotyledons, leaves and stalks.
Phosphatic plants: Plants abounding in nitrogen, seeds.

The investigations which have hitherto been made respecting the inorganic elements of plants, are much too recent, too inconsiderable, and too inaccurate to permit us to draw conclusions from them with regard to the process of nutrition in plants. It appears, however, to be established, that for every species (and variety) certain different kinds and qualities of matter are found so constant, that we may regard them as essential elements for those plants without which their vegetation and their nutrition would be impossible, and that they must, therefore, be offered these in the form of food. We may even maintain that the specific varieties of plants, so far as their nutritive processes are concerned, depend almost exclusively upon the inorganic elements, whilst the organic elements requisite to all plants are alike or nearly alike for all.

When, however, we find all parts of plants which are rich in compounds of the dextrin series abounding also in potassa and soda, and all organs which contain much of the protein compounds containing also almost in equal measure salts of phosphoric acid, we must arrive at the conclusion, that the alkalies have, with the chemical processes of the dextrin series, and the salts of phosphoric acid, with the origin of the protein compounds, a close and essential connection. It further appears that the solidity of the cell walls depends in part upon the inorganic matter received by the plant and deposited in the substance;

and in the Monocotyledons silica, and in Dicotyledons lime and magnesia, appear to be characteristic.*

## II. *On the Absorption of Food and Excretion.*

§ 194. We have now to take into consideration, without regard to their intention, all those processes which occur on the external surfaces of plants, by which they take up matter within their structure, or by which they throw it off.

### 1. *Of the Form of the Matter.*

All matters which plants either take up or throw off, must pass through a homogeneous membrane moist with fluid, the cellular membrane, and must also be soluble in water, as the only universal solvent. Only as fluids, vapours, or gases can they pass into or out of the plant. Insoluble matters can never become the food of plants by undergoing a chemical decomposition outside the plant.

Plants have no stomachs, nor the analogue of a stomach, and consequently they have no digestion. The animal kingdom has a stomach, in order to enable it to convert the nourishment received from a solid to a fluid, from an insoluble to a soluble form; then follows the absorption of the nutriment through homogeneous membranes. But plants must find all the substances requisite to their nutrition already in state of solution; they have no gastric juice by means of which they may chemically decompose and dissolve substances not ready prepared; nor have they salivary glands, in order to maintain the supply of a solvent juice. The organic elements, carbon and nitrogen, are only present as carbonic acid and carbonate of ammonia dissolved in water. Hence vegetation is absolutely dependant upon water as a common solvent. Countries that are entirely destitute of water are incapable of sustaining vegetation, as is the case with Sahara, a portion of the Gobiwüste, &c.; whilst the purest sand, if supplied with water, becomes capable of supporting a vegetation, though it may be of a very poor and unproductive order. Upon the supply of rain from the equator to the poles, and more especially upon the supply of vapour in the atmosphere, the luxuriance of vegetation is strictly dependant.

The inorganic elements, as they are originally found in the firm crust of our planet, are seldom or never soluble. Before they can be used, a chemical process, aided by a mechanical one, must take place; in a word, they must be acted upon by the weather, in order that plants may digest them. From these facts, two opposite considerations arise. The matters which are taken up by plants must be soluble, but they require to be not easily dissolved †, or else they must be very gradually set free from the insoluble matter with which they are in combination, and should be yielded in very small quantities, in a soluble form. Plants

* See Appendix A.,

† Upon this depends the secret of Liebig's patent manure. He maintains that he has succeeded in replacing the easily soluble salts (matters) in the form of difficultly soluble combinations.

stand constantly in need of the inorganic elements of the earth, but only in very small quantity. They need, for example, carbonate of potassa; but a considerable quantity of this salt is either dissolved out of the soil by rain, or by a constant evaporation the water is so concentrated that it exerts a destructive influence on plants. Hence there exists a necessity either that the salt must belong to those difficult of solution, as gypsum, carbonate of lime, &c., in which case all the water taken up would contain the same percentage of salts, because the diminution of the quantity of water is attended with a separation of a certain quantity of the insoluble salt; or else the salts must be delivered, as are the phosphates and carbonates of the alkalies, very gradually by the action of the atmosphere, and subsequently decomposition. This last is the case with silica, which is so difficult of solution, and so quickly resumes its original solid condition. The plants which need this ingredient can only obtain it when it exists in the form of the silicates, or when, by the decomposition of organic substances in the earth, the requisite quantity is set free.

Gases enter into the same category as fluid matters, since all gases that come under our consideration here are more or less soluble in water. The relation also of gases separated from each other by a moist homogeneous membrane is the same, whether they are insoluble in water or not.

### 2. *Of the Form of the Processes.*

§ 195. We must regard the processes of absorption and excretion from three points of view, according to the form of the matter.

1. The absorption and excretion of fluid matter, which embraces the question of the interchange of the matters, and of independent excretion.

2. The absorption and excretion of vapour, which always occurs independently.

3. The absorption and excretion of gases, which is carried on by interchange, and also independently.

These three processes may be called nutrition, perspiration, and respiration, provided we do not suppose them analogous to the like-named processes in animals.

§ 196. The absorption of fluid matters occurs probably mostly, if not always, in connection with a simultaneous excretion of smaller amount, according to the laws of endosmose.

In reference to endosmose, there are three relations of the plant to the media in which it vegetates to be distinguished. The simplest and most natural case is the vegetation of plants in water, or in a soil perfectly saturated with water (as in bogs). In this case, the cell-walls are in immediate contact with the fluid, and receive it by endosmose, so long as no covering prevents it. A trifling difference between the chemical or physical contents of the cells and the surrounding water is sufficient to sustain the endosmotic process.

The second case is that in which the cells come in contact with solid matter, endowed with the property of absorbing water. In

this case the contents of the cells will vary from the absorbed water much more than in the former; for the endosmotic attraction must overpower the resistance with which the water is held in the soil. The most common and important medium in this case is found in the decomposition of vegetable substances rich in carbon, which are known by the collective names of garden-soil, mould (*humus*). It is often found also in inorganic substances, endowed with similar physical properties. The greater or less facility with which they are able to absorb and condense water, carbonic acid, and salts of ammonia from the atmosphere, is important. For this purpose mould is the best possible medium. The great aim of culture should be to endow the earth as richly as possible with the physical qualities requisite to serve the plants that are to grow in it.

The third case is that in which plants vegetate only in the air. It has only recently been discovered with certainty, that this case actually exists in the vegetation of the tropical *Orchidaceæ*. In such plants, the root-sheath appears to supply the place of soil, and they draw their nourishment from the surrounding air.

In all these cases, the absorption of matter by endosmosis is doubtless connected with a process of excretion, though small. Such excretion is produced by the endosmosis of the cell contents and assimilated matter of the plant. The comparison of these with excrements, as matter which the plant has worn out, is perfectly inapplicable, and cannot be supported by accurate investigation.

Up to the present time we know of no other power by which fluid can penetrate into the interior of a cell, than that which occurs as the result of mixing two fluids, separated by a permeable organic membrane, and which is at the present time called endosmose. We cannot, therefore, regard the act of absorption from any other point of view; at the same time, the observations upon endosmosis are only recent, and there are yet many unanswered questions which can only be solved by accurate observation, and all hasty generalisations and hypotheses must be eschewed. The different localities in which plants grow have been well known, but because nothing has been known with regard to the processes of absorption, no distinction of these localities could be made according to the characteristic modes of the absorption of nutriment. No sooner, however, do we see that endosmosis lies at the basis of absorption, than we discover that the above three distinctive modes of it demand attention. The simplest case in which plants are, for the most part, in contact with water, occurs least frequently in the *Phanerogamia*, those plants which have been almost exclusively regarded as the object of physiology; and the results of endosmotic experiments have been applied to these alone. If endosmotic phenomena are regarded, without taking a wide view of the different kinds of vegetation as it occurs in the earth, on stones, in wood, &c., which produce an essential difference in the relation of water to the plant, only the most superficial knowledge can be obtained. It is only by extended observations that we can expect to explain the relations of this subject, and to fill up the hiatus in our knowledge of the subject. Yet all previous vegetable physiologists who have treated of this subject have supposed that a plant is growing in

free water, and applied their results to plants growing in the earth. In the next place, it is necessary to ascertain far more accurately than has hitherto been done, in what circumstances the water is retained in the various soils, and most especially in that form of it called humus. That a difference exists is shown very evidently by the differences existing in the root of a plant, when grown in dry earth and in water. In the last case, the entire surface is smooth; in the first, the cells of the epidermis are more rapidly developed in proportion to the dryness of the earth, and form long papillæ which are insinuated around the smallest lumps of earth. The cells of the roots of plants growing in water consist of proportionably broad cells, the contents of which are exceedingly thin. On the other hand, in plants growing on the land, those parts which take up the nutrient matter are composed of a very delicate small-celled tissue, the contents of which is mostly mucus, which consequently exerts a very strong endosmotic action. This or a similar difference shows, that if the nutrition of the plant is effected through endosmose, that in this case it has to overcome, not only the power of attraction in the mixture, but also the power with which the constituents of the soil retain the absorbed water. In this case the experiment is required to determine what difference takes place in the endosmometer, between the action of a diluted fluid by itself, and the same mixed with a quantity of mould.

In recent times we have received important additions to our knowledge of the physical peculiarities of the substances contained in the soil, and have learned consequently to regard them in quite another light. Generally, the soil consists of various kinds of rocks, decomposed and disintegrated, and also of a quantity of soluble and insoluble, more or less easily decomposable inorganic combinations, mixed with a smaller or larger proportion of organic substances in a state of decomposition. These various organic and inorganic combinations possess, in a very varying degree, the properties of forming looser or more compact masses amongst themselves, of retaining water or allowing it to pass freely through them, of condensing the vapour of the atmosphere, absorbing carbonic acid, oxygen, and ammonia, &c. On these various properties depend, universally and essentially, the fruitfulness of a soil, in so far as it depends on the greater or less facility with which the nourishment of plants is taken up by the process of endosmose. In this relation, the half decomposed organic substance, known by the collective name of humus, is important, as it possesses the properties of absorbing gases and vapour, and retaining moisture for a long time. Wood-charcoal also appears to possess properties of this kind, worthy of investigation; and according to the experiments of Lucas, it would appear to be especially beneficial to certain kinds of plants. It is on account of this substance, apparently, that certain plants, such as *Marchantia polymorpha* and *Funaria hygrometrica*, are almost sure to spring up on the spots where wood fires have been kindled, and their ashes left on the ground. Special researches on this point are demanded by agriculture and horticulture.

The third case mentioned in the paragraph is, I willingly admit, somewhat hypothetical. When we examine the tropical *Orchidaceæ*, as they grow luxuriously in our hothouses, and find that only one or two of their roots adhere by their sides to the bits of cork on which they grow suspended, and consider that the peculiar covering of their roots distinguishes them from all other roots, and that this is composed of a spongy cellular tissue, resembling in its physical properties those bodies which,

like wood-charcoal, absorb gases and moisture from the atmosphere, the expression of the fact in the text seems natural and warranted. This subject suggests a beautiful series of experiments for the purpose of determining the facility possessed by the root-sheaths of absorbing gases and vapour from the atmosphere, and introducing the same to the roots.

Some observations of the earlier experimentalists, and which are perfectly correct, but which were employed for the purpose of forming theoretical views, founded upon the false analogy between animals and plants, and have led to the complete doctrine of the excrements of plants, demand the broadest treatment in the history of our science. They have, however, been recently misused, even by Liebig. The historically important points in this subject are as follows: — Duhamel* was the first to observe that the earth adhered to the spongioles of plants. Brugmans† described a brown substance in the water in which roots were growing. Brugmans and Coulon‡ drew the inference from this, and the well-known fact, that certain plants, as Oats, *Cnicus arvensis*, *Polygonun Fagopyrum*, *Spergula arvensis*, &c., will not grow near each other, — that all plants give out from their roots an excretion, which is injurious to certain other plants. This theory was variously opposed and supported, without any new facts being supplied, when DeCandolle suggested to Macaire Prinsep§ the performance of a new series of experiments to test its value. But these experiments were performed so regardless of securing the essential fact of such a theory, a sound vegetation, that they are entirely worthless. When plants are removed from their natural soil, as in the experiments of M. Prinsep, the roots become injured, and thus the water in which they are placed penetrates the tissues, and necessarily a part of the juices of the sap must flow into the water; and when M. Prinsep adds, that no adulteration of the water takes places if a branch cut off a plant be placed in water, this is so evidently an error that we lose all confidence in his experiments. The worthlessness of the experiment of Prinsep has been pointed out by Meyen (Physiologie, vol. ii. p. 528.), Treviranus (Physiologie, vol. ii. p. 117.), and Hugo Mohl.‖ On the other hand, the experiments of Unger⸸ and Welser¶, which were performed with all proper care and accuracy, gave a perfectly negative result; so that there can be no doubt that an excretion from the root, such as that believed in by DeCandolle, Prinsep, and Liebig, has no existence at all.

It appears almost a necessary conclusion, that if we regard endosmose as the cause of absorption, that excretion from the spongioles, although only to a small amount, must still take place. Such excretion would consist of imperfectly assimilated matters, and some salts, as the special assimilated matters are so bound to the cell that an excretion of them appears almost impossible, as they are never found on the outside of the spongioles, which yet perform especially the function of absorption. But perhaps the assumption of such an exosmose is unnecessary, for

* Natural History of Trees, vol. i. p. 107.
† Dissertatio de Lolio ejusdemque varia specie L. B. 1785
‡ Dissertatio de mutata humorum indole, &c., p. 77.
§ Mémoires de la Société de Genève, vol. v. p. 287.
‖ Dr. J. Liebig's Verhältniss zur Pflanzenphysiologie.
⸸ Ueber den Einfluss des Bodens, p. 147.
¶ Untersuchungen über die Wurzelausscheidung. Tübingen, 1838.

recent researches have shown that endosmose may exist without exosmose, and that the last is entirely dependant on the specific nature of the two fluids. Further observations are needed on this subject.*

§ 197. The excretion of fluid substances has hitherto been but very imperfectly observed. I mention by way of example the following: —

1. The separation of fluid water, through cells which are filled with water, and which do not impede its passage by the thickness of their walls, or by an external covering which might interrupt its escape in any large quantity; e. g. the glands in the pitchers of *Nepenthes*. Whether this water actually escapes in fluid form, we know not; but it is probable, for we find in other cells with slender walls that water must escape as water, and not as vapour, the proof of which is, that it carries with it and deposits a quantity of matter which could not have accompanied it in the form of vapour; for instance, the crystallised sugar found in the flowers of the *Fritillaria* and other nectaries, and the chalk upon the margin of the leaves of so many species of *Saxifraga*.

2. All excretions of peculiar matters on the surface of plants are probably to be classed here; for instance, the numerous clammy juices on account of which we call a plant viscous (*viscosus*).

3. Related to this kind of excretion is the gradual formation of a thicker or thinner layer of wax, the rime (*pruina*) upon the surface of many plants and parts of plants, which, on account of it, are designated pruinose (*pruinosus*), glaucous (*glaucus*), &c. With respect, however, to this last secretion, we might, with some probability, follow out its reaction upon the life of the cells, and thus upon the entire plant, inasmuch as this incrustation on its surface deprives the cells, yet active, of their power of exhalation.

4. Lastly, we may cite the excretion of the volatile oils through evaporation, especially from the leaves, and sometimes the flowers.

With regard to the excretions, we are yet much in the dark. Wherever a perfectly-formed epidermis exists, they only occur as the result of disease; as, for instance, the excretion of juices which are rich in sugar through the leaves, called honey-dew, and the excretion of water-drops in the Grasses, *Araceæ*, in Poplars, and in Willows. There are parts of plants in which no epidermis and no superficial layer of secretion are present to prevent exudations; in such parts the juices formed in the cells penetrate through the membranes, and are found externally. If these juices contain much solid matter, the water may evaporate from them, and the solid matter may accumulate, and, if its physical properties permit, may contribute to the process of exudation by endosmose.

The separation of clear water in pitcher-formed leaves is one of the most remarkable of these exudations. The fact in *Nepenthes* is sufficiently established, though the observations respecting it are few. In *Saracenia* I have never observed water in the pitchers, excepting what

* For the most recent information on this subject, see Matteucci "On the Physical Phenomena of Living Beings," translated by Dr. Pereira. — TRANS.

had been obtained from without; but my observations have been few. How far the observations made upon other plants, and mentioned in their morphology, are accurate, I cannot decide. Respecting the anatomical formation of these parts, and the means by which they separate their water, we know much too little.

I have already remarked, that I can connect no precise and definite idea with the term gland, as referred to a plant. No attentive observer can avoid seeing how different is life in different cells, whether they are found in different plants, or in the same plant, or near each other. It appears to me quite foolish to denominate that cell, or that group of cells, which contains different matter from its neighbours, a gland or organ for secretion; for there are many plants, and parts of plants, which would then consist only of glands. It is ridiculous to call a cell containing volatile oil a gland, and to refuse the name to one that contains red or yellow colouring matter; and should we call the last glands, then almost all petals would consist only of glands. The epidermis would be sometimes an epidermis but sometimes a glandular surface; and with many single cells we should have to admit that they are partially glands and partially not so. If we are to retain the term gland at all, we must apply it to those cells and those masses of cellular tissue which, in consequence of some particular structure, not only contain certain fluids, but also *secrete* them.

The expression gland, then, must be applied not only to the receptacle of secretions mentioned in the next paragraph, but also to definite groups of cells on the surface of plants, which, not covered by epidermis, and consisting of tender cell-walls, allow their contents to exude externally; of such are the glands secreting water in the pitchers of *Nepenthes*, the surfaces secreting chalk in the pits of the leaves of *Saxifraga aïzoon*, *S. longifolia*, &c., and almost all the actually secreting nectaries and appendages of the epidermis.

The last point mentioned in the paragraph has been referred to in other parts of the work, but as yet little is known with regard to it; we have as yet little pursued the fact of the development of volatile oils (scents) in the blossoms and other parts of plants. Some light is thrown on the subject by Morren, "Rapport sur le Mém. de Mr. Aug. Trinchinetti de odoribus florum, &c.," 1839. (Extrait du tom. vi., No. 5 des Bullet. de l'Académie Royale de Bruxelles).

§ 198. The second process to be treated of is exhalation. From those parts of plants which are exposed to an atmosphere which is not already perfectly saturated with moisture, a continual evaporation of water goes on. The process is purely physical, and, according to accurate investigations, it appears to proceed uninterruptedly, according to the dryness and motion of the atmosphere, with the temperature, and the amount of surface exposed to evaporation. It is highly probable that the epidermis permits of no passage to the evaporating water, but that, the evaporation occurring in the neighbouring intercellular spaces, it escapes through the stomates when they are not closed by too strong evaporation and consequent relaxation. From this circumstance the exhaled water is never quite pure, but it contains always a small admixture of vegetable substances which cannot be accurately analysed.

Besides this evaporation of water, we sometimes find in a very

damp atmosphere, and especially in the case of plants that have already exhaled very much, a taking up of moisture, especially through their green parts; but our observations on this fact have been too little accurate and purposeless to admit of a precise explanation of the process.

The study of vegetable exhalation in general requires a repetition and improvement of the experiments made upon it. We need a set of experiments which should show, with the greatest exactitude, the difference between the quantity of water absorbed and exhaled, from which we might decide the quantity used for the nourishment of the plant. If the amount of oxygen exhaled with the water was also obtained, we should probably be able to arrive at conclusions respecting the nature of the chemical processes carried on within the plant. We have yet to ascertain the relation of the exhalation of the wall to its absorption. The fact of its absorption (by other means than the root) has been established by Hales, but we are still quite in the dark as to the manner. An accurate knowledge of these relations is so much the more to be desired, as the evaporation and absorption of water with the tension of the vapour must exert an influence upon the absorption or exhalation of the several kinds of gases. Yet in the experiments made upon the so-called respiration of plants, this has been lost sight of.

We know nothing of the organs through which exhalation is effected. To myself it appears improbable that the living epidermis should be permeable to water and the vapour of water, except through the stomates (see § 36.).

It is an established fact, that all evaporating water carries with it some portion of the matter which it held in solution. This is seen in the vapour of the ocean. It is probable that no water exhaled from plants is absolutely pure. But no accurate analyses have been made on this point.

The natural consequence of this exhalation of water from the green parts of plants which are exposed to the air, is the continual concentration of the juices in the cells which lie next the evaporating surfaces. By this, the endosmose of the cells which do not exhale undergoes a change, of which we shall have to speak hereafter.

The information which we possess respecting the exhalation of plants is chiefly found in the experiments of Hales *, Guettard †, Sennebier ‡, Schübler, and Neuffer.§

The strange tendency always to attribute to vitality something different from the physical powers, has introduced into the doctrine of the transpiration of plants a distinction between evaporation and exhalation; the first being supposed to take place in dead plants and the last in living ones. I can find no distinction in this case in the facts, but merely in the words.

I will here add some facts upon the quantity of water exhaled by plants.

According to Hales ‖, a sunflower evaporated daily 1·25 lb. of water:

* Vegetable Statics.

† Mémoires de l'Acad. des Sc. de Par. Ann. 1784. p. 419, *et seq.*

‡ Physiologie végétale, vol. iv. p. 56.

§ Untersuchung über die Temperatur der Vegetabilien und verschiedene damit in Verbindung stehende Gegenstände. Tübingen, 1829.

‖ Vegetable Statics.

now let us allow to each of these plants 4 □′ space of soil; then upon the old Hessian acre there would stand 10,000 plants, which in 120 days would exhale 1,500,000 lbs. of water.

A cabbage * exhaled in twelve hours of the day 1 lb. 6 oz. of water: now if, according to Block, each plant occupies 5 □′ of soil, and if we reckon an inferior expenditure for the night, yet the plants on an acre would exhale 1,200,000 lbs. of water in 120 days.

A dwarf pear-tree, according to Hales, exhaled in 10 hours of the day † 15 lbs. of water. Allowing for each such tree 20 □′ of soil, the trees of an acre would exhale 3,600,000 lbs. of water, and probably another third of the quantity might be added for the grass between the trees, which would make for the acre almost 5,000,000 lbs. of water.

An acre of 40,000 square feet, planted with hops, exhaled in 120 days 4,250,000 lbs. of water through the hops alone.‡

A square foot of soil covered with *Poa annua* exhaled, according to Schübler §, daily, on an average, during the summer, 33·12 cubic inches of water: thus an acre of meadow land about 6,000,000 lbs.

§ 199. The relation of plants to the gases of the atmosphere has been least of all investigated or understood. Under this head the following processes claim attention.

1. A fluid that comes into contact with a gas, or that is only separated from it by a membrane saturated with the same fluid, absorbs, according to the specific nature of the gas and the fluids, a definite measure of the gas, corresponding to the density of the volume and the pressure under which the gas stands. Thus 100 vol. water at 28″ barom. and 15° C, will absorb 6·5 vol. oxygen, 4·2 vol. nitrogen, 106·0 vol. carbonic acid; 100 vol. of sugar and water of 1,104 sp. gr. will absorb 72 vol. carbonic acid; 100 vol. gum water, 1,092 sp. gr., 75 vol. carbonic acid.

2. When a fluid contains more of a gas than, according to the nature of the gas, and the pressure under which it stands, the fluid can hold in solution, the superfluous gas will escape. It will be the same whether the fluid is free or is covered with a membrane saturated with its own moisture. Since water can only hold in solution 6·5 vol. per cent. of oxygen, and a solution of gum or sugar, similar to the contents of the cells, can only hold 4·6 vol. per cent. of oxygen in solution, it follows that oxygen must escape from the surface of the plant when the juices in the cells contain more than their due proportion of this gas.

3. When a fluid which is free, or covered merely by a membrane saturated with itself, and is already mixed with as much of some gas as it may be able to take up, comes into contact with another gas, an interchange takes place between the two gases; a part of that which was first absorbed escapes, and a portion of the free gas is taken up in its place, and this in proportion to the solubility of the two gases.

* Vegetable Statics, p. 7.
† Ibid. p. 17.
‡ Ibid. p. 19.
§ Meteorologie, 74.

4. Fluids that have chemical affinities with certain gases attract them when they come into contact with them, either free or through a membrane saturated with the same: thus, for example, volatile oils absorb oxygen in order to form resin, &c.

5. Every solid body condenses vapour and gases upon its surface. It does so more largely if it is pulverulent, and still more so if it is porous. Recently-charred wood has this property in the most striking degree. One vol. of box-wood charcoal absorbs 90 vol. of ammoniacal gas, 55 vol. of sulphuretted hydrogen gas, 35 vol. of carbonic acid gas, 9·25 vol. of oxygen gas, 7·5 vol. of nitrogen gas. Humus comes nearest to charcoal in this respect. Water expels a part of the absorbed gases. The entire parenchyma of a plant being permeable, by means of the stomates communicating with the intercellular passages and the atmosphere, makes the plant resemble such porous bodies.

The labours of experimentalists on these physical relations are far from complete. The experiments of Alton *, Theod. de Saussure †, Graham ‡, and Mitscherlich §, only embrace particular points of the enquiry.

When we pass from the simple experiments with one gas and one fluid, or one gas with another, to a mixture of gases and fluids, which is the case in plants, the question becomes more complicated than even our comprehension or experimental art can embrace.

The most simple, and perhaps also the most important relation to be observed here, is the escape of gases from a fluid which, while subject to a certain pressure, held them in solution.

The importance of this fact is seen, as it must regulate the formation of the nutrient fluid, and the absorption of gases through solid porous bodies, and especially through charcoal, humus, and clay.

The possible influence of these laws upon the life of the plant will be seen in what follows.

§ 200. We have now to place certain phenomena of vegetable life, which have been more or less well observed, in connection with the following laws: —

1. The germinating seed takes up a certain quantity of oxygen, and gives off a considerable quantity of carbonic acid.

2. After the period of germination, the plant exhales, during the day and in the sun-light, oxygen from its green surfaces, and takes in carbonic acid through the same parts. By night the process is reversed; carbonic acid is exhaled, and oxygen gas is absorbed.

3. All parts of the plant, not having a green colour, as the bark and the root, absorb oxygen gas and exhale carbonic acid gas.

4. The filaments in flowers absorb, in a very short time, an immense quantity of oxygen gas, and give out in exchange carbonic acid gas.

* Gilbert's Annal. vol. xxviii. p. 390.
† Ibid. vol. xxxvii. p. 163.
‡ Elements of Chemistry.
§ Lehrbuch der Chemie, vol. i.

5. Succulent fruits also, in the period after ripening, absorb oxygen gas, and give out carbonic acid gas.

6. Almost all the parts of plants absorb, under some circumstances, nitrogen from the atmosphere, and exhale it again.

7. Hydrogen also is exhaled by plants, as we know from Humboldt's experiments on fungi.

The experiments which have been made to ascertain the relation of plants to the atmosphere, we owe chiefly to Hales*, Bonnet†, Priestley ‡, Ingenhousz §, Sennebier ‖, Woodhouse ¶, Th. de Saussure**, Link††, and Grischow.‡‡ They may be arranged in three groups, except the old experiments on some water plants, which require to be repeated with extreme accuracy. The first group embraces the experiments in which leaves or stalks, cut from the plant, have been observed. These are worthless; for it has never been ascertained how much air, and what other matters these parts contained within themselves, nor what changes were being carried forward in the interior, nor how long the experiments were continued, &c.

The second group of experiments contains those in which entire plants, vegetating in water or soil, were enclosed in a receiver. These experiments also, the greater part of which were performed by De Saussure, are quite useless, since we have no data whence we may learn how much of the changes produced in the atmosphere were wrought by the leaves, and how much through the soil and roots. The third group is that alone which can yield useful results. In these experiments the green parts of plants were enclosed in a receiver, without the plant being withdrawn from its natural place, and the air in the receiver was that of the atmosphere. To this group belong the experiments of Woodhouse, Saussure, Link, and Grischow.

These last experiments gave the rare result, that the plants, after long vegetation in confined air, neither changed the quality nor quantity of the air by their green parts. Hence there must have existed some fault in connection with them, since the result was an impossibility. The principal mass of the matter in the plants contained less oxygen than the mixture afforded by the soil could have enabled them to take up. In whatever way vegetation goes on, the final result must be the disengagement of oxygen gas, which, when exceeding in quantity the measure which can be held in solution by the fluids of the plant, must escape. The most recent experiments of Boussingault go to prove, what was before known, that plants absorb carbonic acid through their green parts in

* Vegetable Statics.

† Rech. sur l'Usage des Feuilles dans les Pl. (1754), p. 24, et seq.

‡ Experiments and Observations relating to various Branches of Natural Philosophy, with a Continuation of the Observations on Air (1779), vol. i. p. 1, et seq.

§ Versuche mit Pflanzen, wodurch entdeckt ward u. s. w. A. d. Engl. 1780; und: Ueber die Ernährung der Pflanzen u. s. w. A. d. Engl. von G. Fischer, 1798, p. 53 ff. Experiments upon Plants, and an Essay upon the Food of Plants and the Renovation of Soils. London, 1796.

‖ Physiologie végétale (1801), vol. iii. pp. 104—148.

¶ Gilbert's Annalen, 1803, vol. xiv. p. 351.

** Chemische Untersuchungen über die Vegetation; übersetzt von Voigt, 1805.

†† Grundlehren der Anatomie und Physiologie. Göttingen, 1807. P. 283.

‡‡ Physikalisch-chemische Untersuchungen über die Athmungen der Gewächse und deren Einfluss auf die gemeine Luft (1819).

the light of the sun. Boussingault enclosed the branch of a vine in a receiver, through which, by means of an aspirator, air containing a known quantity of carbonic acid was admitted, and after being exposed to the action of the plant, the quantity of carbonic acid was measured by means of an alkali; whilst at the same time the same air, without having come into contact with the plant, proved its carbonic acid contents. The result was, that half the carbonic acid of the air was absorbed by the plant. The absolute quantity of the air which, in a definite time, came into contact with the plant, and also the absolute quantity of carbonic acid, were not measured in this experiment.

I must here also object even to the most accurate experiments of De Saussure. Plants vegetating in the light absorb carbonic acid and exhale oxygen gas; but the quantities of oxygen and of carbonic acid do not stand in any equal relation to each other in his experiments. The following plants, instead of absorbing an equal volume of 10 cubic centners of carbonic acid gas for each 100 cubic centners of oxygen gas which they exhale, absorbed the following quantities of carbonic acid:

| | | |
|---|---|---|
| *Vinca minor* | 147·6 | cubic centners. |
| *Mentha aquatica* | 137·2 | „ |
| *Lythrum Salicaria* | 123·1 | „ |
| *Pinus genevensis* | 123·6 | „ |

Of the entire amount of oxygen received, they retain from $\frac{1}{3}$ to $\frac{1}{5}$.

The facts which have heretofore been recorded lie as yet unexplained before us. There is no present possibility of bringing them into harmony with our physical knowledge, for both the one and the other are in an incomplete condition. Our next effort must be to pursue those phenomena which we find exhibited in certain definite groups of cells, or which are manifested within certain determinate portions of time, in order to learn to separate them from what belongs unceasingly to the vegetation of each individual cell.

### III. *Assimilation of Food.*

§ 201. The principal substances absorbed by plants are water, carbonic acid, carbonate of ammonia, and certain inorganic salts. The plant draws all these from the soil by the spongioles. It receives carbonic acid from the air through the leaves. In what relation these two methods of absorption stand to each other, and to the necessities of the plant, is unknown to us. The exhalation and the interchange of gases is carried on in connection with the air immediately in contact with the surface of the plant, and also between the cellular tissue and the intercellular passages, from whence gas and vapour escape through the stomates.

As the great mass of substances which form the plant contain less oxygen than the plant absorbs, it follows of necessity that during the process of assimilation oxygen is set free. Probably neither oxygen nor water are decomposed directly, but a series of combinations takes place, from which, at certain points, or else finally, oxygen is set free. For example, a small portion of the oxygen in the green parts of plants appears to originate in a

decomposition of the starch or similar matters into wax. It would appear that the exhalation of oxygen, and the absorption of carbonic acid gas, never stand in immediate relation with each other.

The formation of carbonic acid by other than the green parts of a plant, as the bark and the root, is no vital process, but is the commencement of a process of decomposition (decay). The formation of carbonic acid during germination and flowering depends, as in fermentation, upon a decomposition of organic substances; it thus serves the vital processes without being itself a process of organic development.* The absorption of oxygen, or the oxydation of secreted matters, as the volatile oils, tannin, &c., is entirely independent of the essential life of the plant.

After a long night of physical and chemical ignorance, the dawn of a true theory of the nutrition of plants is breaking upon us, not without having been dreamed of in the previous darkness. "Plants absorb the crude sap from the soil; it is then conveyed upwards through the spiral and porous vessels to the leaves, where it is assimilated; from whence it is sent down to the bark, in order to form buds, leaves, and roots." "The leaves absorb carbonic acid gas, decompose it, and give out the oxygen gas which it contained."

This was the substance of the dream, of which the least possible promises to be realised; it was only a dream-picture, not founded on observation or inductive enquiry, and therefore of no value.

In the first place, there is no such thing as crude sap. It cannot, therefore, be carried to the leaves to become assimilated. From whatever part and at whatever time we examine the sap of a plant, we find that it contains organic principles which cannot come from the soil, because they do not exist there; such are sugar, gum, malic, citric and tartaric acids, albumen, &c. These substances are diluted with a good deal of water, and mixed with a little carbonic acid and carbonate of ammonia, which are contained in the water of the soil. Even in the cells of the roots, which first receive the moisture of the soil, it is chemically changed, assimilated, and the sap is most decidedly not flowing in special vessels, but passing upwards from cell to cell, and thus it is in every new cell which is being developed by the formative chemical processes; nothing remains for the leaves to assimilate. That the leaves in their natural growth absorb carbonic acid from the air was a pure invention, for, until Boussingault, no one obtained proof of this by experiment. The fact appears to be fixed by Boussingault, but this proves nothing for the assimilating power of the leaves. From whence then comes this carbonic acid? Not from the cells in which chemico-vital processes alone are carried on, but from the intercellular passages, which in the largest plants communicate one with another, from the extreme points of the roots. The conclusion that the carbonic acid found in the leaves is consumed by them is about as rational as the inference would be, from the respiratory movements of the nose and mouth, that the brain performed

* At the meeting of the British Association at Cambridge in 1845, I read a paper before the Section of Natural History, the principal object of which was to give the explanation alluded to in the text, of the facts which occur in the germination of plants. See Transactions of Brit. Ass. for Adv. of Sc., 1845. — Trans.

the functions of the lungs. If, also, we may assume with Mulder, that a part of the oxygen which is thrown off by the leaves results from the change of starch into wax, then this proposition sinks into comparative insignificance. We may calculate roughly how much oxygen is thus set free. An acre of clover yields in a year, according to Boussingault, 2,153·5 lbs. of clover, which contains:

| | |
|---|---|
| 1020·68 lbs. | carbon. |
| 107·70 | hydrogen. |
| 814·04 | oxygen. |
| 45·21 | nitrogen. |

If we suppose that all the nitrogen was derived from ammonia, and all the carbon from the carbonic acid, we should arrive at the following results:—

| | | | |
|---|---|---|---|
| 1,020·68 C | + | 2,670·74 O | =carbonic acid. |
| 45·21 N | + | 9·26 H | =ammonia. |
| 107·70 H | + | 9·56 H + 786·00 O | =water. |
| 814·44 O | − | 7,8600 O | = 28··040. |
| 2,670·74 | − | 21·04 | =2642·7 O, which must be excreted. |

But, according to Mulder, 10 eq. of starch = 20,420·0, exactly 3 eq. of wax (=13,070·2) + 3,153·0 water + 4,197·0 oxygen, or the excretion of 2,642·70 lbs., agrees to the formation of 8,229·8 lbs. of wax, and the decomposition of 12,762·3 of starch. But 21,53·5 lbs. of dried clover could not possibly contain 8,229·8 lbs. of wax. It would afford, when extracted by ether, about 86·14 lbs. of fatty matters. The excretion, then, of oxygen, in consequence of the change of starch into wax, agrees with about a hundredth part of the collective process.

But take whatever view we will of the nutrition of plants, it remains certain that a skilfully cultivated soil never becomes poorer in organic compounds containing carbon, but even richer; thus proving, setting aside the loss of carbon from the soil by decomposition, that the greater quantity of carbon in the harvest is not derived from the manure, but from carbonic acid. An acre of land, in good culture, yields 790·8 lbs. of carbon more in the harvest than is contained in the manure; to fix this quantity of carbon not less than 2,000 lbs. of oxygen would be set free, which, according to Mulder's hypothesis, would represent the formation of 6,300 lbs. of wax.

On such necessities hangs the doctrine of the nutrition of plants, in order to account for the excretion of 2,000 lbs. of oxygen, we are referred to a process which will not yield more than 30 lbs., and the presence of 2 lbs. of sulphur is derived from 400 lbs. of gypsum, employed in the culture of the plants, and which contain 90 lbs. of sulphur. Of the botanists and agriculturalists who derive the carbon of plants from humus and manure, the former have forgotten their own experiments, the latter never knew them. The tables of Boussingault were not required, as every German manual of agriculture contains calculations of the quantities of manures and harvests which, if the elementary substances had been properly calculated, would have afforded results that would long since have pointed out the true laws of nature. All who have written upon this subject have failed to take a general view, and on this account all earlier works, some few of the oldest excepted, are utterly useless. Whoever writes on these matters ought to give new and exact researches, in order to save himself and others from error.

The absorption of oxygen by plants at night, which has been confirmed it appears by experiment, is explained by Liebig as a process of oxidation of the volatile oils. But this process must also go on in the day, and therefore it fails as an explanation.

The researches upon the absorption of nutriment in plants are of little worth, because they have proceeded from prejudices, often of an opposing nature, without the least regard to the natural circumstances of vegetation. Land-plants do not grow in water, or in a soil saturated with fluid. The moisture of the soil exists under peculiar circumstances, upon the nature of which there is an absence of all investigation. It is absorbed by solid substances, and can only be retained by some essential modification of the process of absorption. There is no lack of bad experiments upon the matters which are absorbed, but not one good chemical examination of the nature of the moisture ordinarily found in the soil, and which is the true food of plants. The consequence is, that we know nothing certainly of the processes that go on in the interior of the plant, in nutrition and assimilation. The best thing that has been said on this subject appears to me to be a remark of Liebig, who says that the carbonates of the alkalies are apparently gradually converted into salts of vegetable acids, containing little oxygen. The malates are, through a deoxidising process in the potash and dextrin, probably destroyed; but there is no experimental proof of this.

Upon the origin of particular compounds we know nothing. Liebig, when he speaks of the possibility and probability of the decomposition of carbonic acid, says that this process must take place, in every case, during the formation of fatty matter. We might admit this if we could form fats out of carbonic acid and water; but we cannot do this, and all analogy leads us to the much more probable conclusion that the fats are formed out of the compounds of the dextrin series. To calculate the various possible combinations of the elements on paper is not very difficult, but for affording a knowledge of what really takes place in nature, such a proceeding is entirely useless. That some few inorganic compounds are converted into organic compounds during the nutrition of plants, we know with absolute certainty; that during these changes the inorganic salts play an important part, is probable. But what organic compounds are first formed, — through what special chemical processes they originate, is at present entirely unknown, although it must form the foundation of a true theory of nutrition. In recent times we have received from the researches of Liebig, Mulder, Dumas, and others, numerous schemes and explanations of the various metamorphoses of the organic matters in plants. But by far the most extensive part of the question, and for vegetation generally the most important, has been hitherto untouched: here is a wide field for united exertion. The chemist, often with great industry, builds up a theory which one glance through the microscope dissipates. The physiologist exercises great acuteness in bringing his observations into relation, and when he has done, the chemist tells him it is chemically impossible. Thus both time and energy are lost.

There is another circumstance to be referred to in this place, which renders observations on plants difficult, and which ought to be regarded in the selection of plants for experiment. Although plants, as such, must exist according to the morphological relation of their physiological elementary organs, yet individuals of one and the same species contain, both qualitatively and quantitatively, a great variety of elements, and

even they absorb sometimes one kind of matter and sometimes another. This is not exhibited at all in the form of the species of the plant, for this remains the same in all circumstances. The change takes place in individual cells. Thus, in the same cellular mass, say of 1000 cells, there will be in one case 200 containing starch granules, and 400 containing oil; in another there will be 500 containing starch, and only 100 oil: but the form of the plant suffers not the slightest change; or, what is more frequently the case, the relative quantity of particular substances becomes changed: thus, particular cells will at one time contain 7 per cent. of gluten and 70 per cent. of starch, and at another time will contain 35 per cent. of gluten and 40 per cent of starch. For every species of plant there are definite quantities of certain matters necessary for its existence, but it frequently takes up matters which are not necessary for its existence, and a superfluity of matters which are necessary for its existence; and thus both the quantity and quality of its contents are changed. This, then, is a problem for pure empirical research—how far plants will bear departures in the quality and quantity of the normal constituents of their food. Many plants appear to require a very precise diet, which will account for their limited distribution and the difficulty of their culture, whilst others seem to adapt themselves to all circumstances, and present great variety in their contents. Thus the composition of the milky juice of the *Papaver somniferum* (Opium), according to Biltz, Mulder, and Schindler, is as follows:—

| | | | | | |
|---|---|---|---|---|---|
| In Morphia, | from | 2·842 | to | 20·00 | per cent. |
| Narcotin | „ | 1·30 | „ | 33·00 | „ |
| Caoutchouc | „ | 2·00 | „ | 6·012 | „ |

It is also well known that the plants which yield caoutchouc afford very variable quantities, according to the varying circumstances under which they grow. If we also add to this the fact that plants yield poisonous or inert secretions according to their locality, we cannot but conclude that certain substances appear or disappear in the plant when external circumstances are given, without altering their external character. This great variability in the composition of plants must always be regarded in experimenting upon the vegetable kingdom.

### IV. *External Conditions of the Absorption and Assimilation of Food.*

§ 202. As external conditions of the absorption and assimilation, we may here point out:—

I. The soil in which the plants root. This requires, besides its chemical contents of inorganic matter for food, also certain mechanical and physical properties in order to render the nutrition of plants possible. Hence clay and humus, as substances that absorb gas and vapour, are important.

Next to the consideration of the materials themselves of the food of plants, in order to form a true theory of the culture of plants, and the understanding the processes of nutrition, there is nothing so important as the investigation of those relations upon which the health of the plant is essentially dependant, and which do not afford the materials of the

food. For agriculture these circumstances may be divided into those over which man exercises entire or great control, and those over which he has no influence, and which he must take as they come, or which at most he may press into his service by a knowledge of their perfect regularity. These last the child-like man beautifully, and in a certain sense truly, calls "the blessing of Heaven." But for the scientific consideration of this subject we need another division, in order to arrange the few facts which are at present known to us. I shall consider, first, the soil; and, secondly, the imponderables, in their relation to the nutritionary process in plants.

1. *The Soil.* — By soil I understand here the earth in the narrowest sense; all that is necessary has been said above about water and air. We must regard the soil, in relation to the plants growing in it, in a threefold sense: —

*a.* According to its chemical constitution, as it contains the inorganic food of plants.

*b.* According to its mechanical properties, through which it is fitted for the penetration of the roots, and for holding them firmly.

*c.* According to its physical peculiarities.

The first point has been already dwelt upon; for the second we have neither facts nor laws. Climate serves the wild vegetation; this determines the distribution of plants. In agriculture we change the mechanical constitution of the soil through the plough, the harrow, and manure. It is to the last point, then, we shall address ourselves here.

Water, as the universal solvent of the nutritive matters, is indispensable, and much unnecessary trouble has been taken to calculate the quantity of water, as rain or snow, that falls upon the surface of the earth. The free water in the soil is seldom beneficial to plants, and it is a well-known fact, that when a soil is saturated with water it becomes an injurious locality for the great majority of plants, and that only bog plants, or those which grow in water, will exist in it. In those portions of the earth's surface which produce the most plants, water is only occasionally present (as after rain, &c.) as a coherent fluid. The normal condition of water in the soil is as hygroscopic water or absorbed vapour.* The complete independence of vegetation of the atmospheric precipitation of rain in a liquid form, is seen in the vegetation of the Oasis, and of the cloudless coasts of Chili and Peru (see Darwin and Loudon), and in a small way in the experiments of Ward.† The sand of the Sahara produces no vegetation, not because no rain falls upon it, but because it has not the power of condensing aqueous vapour.‡ Of the water which falls as rain, very little is used directly by the plant: the greatest part runs

* How essentially this condition of the water in the soil is connected with chemical processes, and thence with the preparation of the food for plants, is shown by Boussingault (Econ. Rur. vol. ii. p. 199.) in a striking manner, in an explanation of the value of gypsum (sulphate of lime) as a manure. Whilst in the presence of fluid water gypsum and carbonate of ammonia are mutually decomposed, in ordinary soil exactly the contrary takes place, and carbonate of lime is decomposed by sulphate of ammonia.

† On the Growth of Plants in closely glazed Cases: London, 1842. Ward's plan of growing plants in closed cases, where the moisture exhaled by the plant is constantly again absorbed from the soil, is now very generally come into use in Europe, for the purpose of cultivating tropical plants, and with the best possible results. Ward relates cases in which he has kept plants, especially Ferns, in a state of luxurious vegetation for upwards of nine years in a sealed flask.

‡ Perhaps also on account of the absence of aqueous vapours in the air. I know of no hygrometric experiments on the Sahara and other deserts.

off, or is evaporated into the atmosphere, whilst another part sinks into the earth and feeds the springs. There are but few observations upon the quantity of water needed by plants, but the facts supplied by Hales and Schübler show that rain, after making allowances for that which flows away and is evaporated, does not supply more than a tenth part of what is necessary. It is unaccountable and inexcusable, that not a single botanist since the time of Hales should have taken up and carried on his experiments. If we take the previous calculations (page 501.) of the quantity of water required by plants in England, which is deduced from Hales' experiments, and which agree with those of Schübler on *Poa annua*, we shall obtain the following approximative results. According to Schübler *, there falls in England, upon the acre of 40,000 □ F., at the utmost 1,600,000 lbs. of water during 120 days of summer. According to the researches of Dalton, Müller, Berghaus †, and Dausse ‡, at least a third part of this water flows away into the rivers, but it is probably more § than this, as the great rapidity of the flow of the water in steep, hilly, and mountainous regions is not sufficiently taken into consideration. A considerable, but not accurately to be estimated quantity of water evaporates immediately after the fall of rain, as the vaporous state of the atmosphere indicates. From this it would appear that at the most there is left disposable for plants and future evaporation 800,000 lbs. of water on the acre. Now this quantity of water, according to the preceding experiments, would cover not more than two-thirds of the demand of an acre of Cabbages, half of the demand of an acre of Sunflowers or of the Jerusalem Artichoke (*Helianthus tuberosus*); the fourth of a fruit-garden, the fifth of a hop-garden, and about the seventh or eighth of a meadow. It must be recollected, that here only the water is taken into calculation which is given out from the plants and weeds growing in a meadow, but that which is afforded by the evaporation of the soil itself cannot amount to less than 2,000,000 of lbs. for an acre. Thus much is very evident from these calculations, that the quantity of rain that falls upon the earth is no more a measure of the quantity needed or consumed by the plant, than is the quantity of humus an index to the fertility of the soil. We may learn from this that the quantity of rain which falls in a given region is not a measure of its fruitfulness, but the quantity of moisture, the absolute and relative quantity of vapour, which yearly, and especially during those months which are most important for vegetation, is contained in the atmosphere.

Thus much then is certain, that the soil, in order that it may nourish plants, must absorb a large quantity of water from the atmosphere, and must possess the necessary properties for that purpose. This property is only possessed to a great extent amongst the original constituents of the soil by clay, so that a soil free from clay is unfruitful. But the primitive vegetation of the earth enriched the soil, by its death, with a substance (humus), which also possesses this property, and which in proportion to its abundance produces a luxurious vegetation without affording from its own substance any part of the nourishment of the

* Meteorologie, p. 130.

† Berghaus Länder und Völkerkunde, vol. ii. pp. 24, 227.

‡ Studer Lehrb. d. physikal. Geog. p. 85.

§ The calculations of Berghaus, for the flow of atmospheric water into the Rhine, gives a result of three-fourths; those of Studer for the same river, four-fifths. But the calculations of Berghaus for the Weser show a larger quantity of water carried away than falls from the atmosphere.

plant. In this way the ability of the soil to support a prolific vegetation is dependant on those climatic influences which rapidly determine the death of plants, or the parts of plants, and converts them into humus. Herein we see the foundation of the variety of the vegetation in different parts of the earth, and the determining cause of the richness of a tropical vegetation.

The industrious Schübler * has made a series of experiments, in order to reduce to number the capacity of various kinds of soil to absorb water from the atmosphere. The results are contained in the following Table :—

| Kinds of Earth. | 1000 Grains of Earth distributed over a Surface of 50 Square Inches absorbed in — | | | |
|---|---|---|---|---|
| | 12 Hours. | 24 Hours. | 48 Hours. | 72 Hours. |
| | *Grains.* | *Grains.* | *Grains.* | *Grains.* |
| Quartz Sand . . | 0 | 0 | 0 | 0 |
| Limestone Sand . | 2 | 3 | 3 | 3 |
| Gypsum . . . | 1 | 1 | 1 | 1 |
| Loam Clay (Lettartiger Thon) | 21 | 26 | 28 | 28 |
| Muddy Clay (Lehmartiger Thon) | 25 | 30 | 34 | 35 |
| Resonant Clay (Klangartiger Thon) | 30 | 36 | 40 | 41 |
| Pure grey Clay . . | 37 | 42 | 48 | 49 |
| Fine calcareous Earth . | 26 | 31 | 35 | 35 |
| Fine Magnesia . . | 69 | 76 | 80 | 82 |
| Humus . . . | 80 | 97 | 110 | 120 |
| Garden Mould . . | 35 | 45 | 50 | 52 |
| Field Mould . . | 16 | 22 | 23 | 23 |
| Slaty Marl . . | 24 | 29 | 32 | 33 |

These experiments were performed in an atmosphere saturated with moisture at a temperature of from 12° to 16° R. (59° to 64° Fahr.). In order to apply these results, we want three other series of experiments on the absorbing power of these substances. 1. According to varieties of temperature; 2. The thickness of the layer of earth; 3. The degree of moisture of the air. Should we now attempt to apply Schübler's results (which are certainly unsatisfactory) to a soil 12″ deep, we should find that plants were supplied during a period of 120 days with the enormous quantity of eighteen millions of pounds of water.

But water is not the only nor the most important portion of the food of plants. They require carbonic acid gas and the volatile salts of ammonia, which must be derived from the atmosphere; they are absorbed, the carbonic acid partly, and the ammoniacal compounds probably entirely, by means of the roots. The greater proportion of these substances which are brought down by the rain are also evaporated with the water; hence the necessity of the presence in the soil, in the form of clay and humus, of media to convey them to the plant. In all agricultural estimates of the value of the soil, the entire decision turns upon the contents of clay and humus. Some of the best wheat soils often do not

* Agrikulturchemie. 2d edition. By Krutzsch. pp. 2, 84.

contain a trace of humus, and their only value consists in the quantity of clay they contain.

There is a prejudice extant among some people, and which unsuspiciously lies at the foundation of their view of the nutrition of plants, and that is, that cultivated plants upon prepared soil vegetate under more advantageous circumstances than plants growing wild. The fact seems to be directly the contrary, for in the culture of the land most plants are placed in circumstances so directly opposed to the natural circumstances of their growth, that we have to employ all the art of agriculture for obviating their injurious action. The problem of agriculture consists in covering a given area with plants of the same species. To this end we must first destroy the whole natural vegetation of the soil (uproot the soil), and as much as possible prevent every new growth upon the soil. The mechanical processes necessary for this are attended with injury to the vegetation, which is increased by our yearly carrying away as harvest those products which, with plants growing wild, would remain upon the soil. The working up of the soil, and allowing it to lie fallow, acts injuriously by exposing it to the action of the weather and desiccation from the sun; at the same time, the decomposition of the substances drawn by the water from the humus is accelerated; and, lastly, the naked and loose earth is exposed to the constant washing of the rain. Finally, cultivated plants sustain injury from the fact, that the soil is covered with a species for which it is not naturally adapted, and consequently the produce is never so large as it might be.

Very different are the results the nearer the culture of the field approaches that of the garden. In this case the cultivated plants have strikingly the advantage of the wild plants of our climate. The garden soil is distinguished by two peculiarities which arise out of the action of excessive manuring. First, it contains all the inorganic elements in the greatest quantity and the most favourable form that is combined with easily decomposable organic substances. Secondly, it has, on account of the quantity of humus it contains, the capacity of supplying the growing plants with the organic elements it contains, and especially with water in the greatest quantity and constancy. The latter property ensures a luxuriant vegetation; whilst the former, on account of its favouring the chemical processes in the plant, ensures an opulence of form which is quite impossible in a poorer soil. Indeed, we never see in the virgin soils of nature, nor in our fields, the rich variety of forms which are observed in our gardens, and in some instances the action of the circumstances producing these varieties is so permanent that they can be propagated by seeds. It is impossible that these influences should lose their activity even where they are formed without the assistance of man. Thus, we find in the tropics, where the conditions fail for forming a good garden soil, that there, as with us, wildernesses, or a wearisome monotonous vegetation, prevail. On the other hand, we find that where in the tropics the conditions of a rich garden soil prevail, that there we have the greatest profusion of forms and the most luxuriant vegetation. In this way many varieties produced in the course of centuries may become permanent forms, whilst the forms of a less favoured climate may be only the residue of an earlier period in the history of the earth: so also in higher latitudes, even at the poles, the peculiarities of the atmosphere may produce conditions which are now only found under the tropics.

The power possessed by the soil of becoming heated by the sun exerts as much influence on the health of the plant as its power of retaining gases and vapour. The warmth of the soil acts upon plants entirely independently of the temperature of the air, and frequently requires to be much higher, in order that plants may flourish. Unfortunately, on this subject we have but few observations, and these principally relate to our hothouses and tropical districts.

The following Table gives an approximation to the temperature of the soil borne by plants without injury: —

| Place. | Temperature of Soil: Centigrades. | Remarks. | Observer. |
|---|---|---|---|
| Cape of Good Hope . . | 70·5 | In the Soil of a Garden | J. Herschell. |
| Egypt . . | 56·00—62·25 | — | Edwards and Collin. |
| In the Tropics | 52·25—56·7 | — | Humboldt. |
| France . . | 47·75—50 | — | Arago. |
| Lantao (China) | 45·00 | Water in Rice-Fields | Meyen. |

The following interesting Table I have taken from Schübler. The columns A. relate to observations made by Schübler in his own garden at Tübingen, 1010 Paris feet above the level of the sea, with a southern aspect, and at mid-day, between the hours of twelve and one o'clock. The columns B. give the average of daily observations made in the Botanic Garden at Gent in 1796, 1252 Paris feet above the level of the sea.

| Months. | A. Average Temperature. | | B. Average Temperature. | | | |
|---|---|---|---|---|---|---|
| | Surface of the Earth. | Air in the Shade. | Surface of the Earth. | 3″ under the Earth. | 4′ under the Earth. | Air in the Shade. |
| January . | + 9·8 | — 3·3 | + 4·89 | + 2·88 | + 3·28 | + 2·73 |
| February . | + 24·1 | + 4·9 | + 6·10 | + 3·46 | + 2·92 | + 2·17 |
| March . | + 30·0 | + 6·5 | + 9·42 | + 4·97 | + 2·72 | + 2·71 |
| April . . | + 39·8 | + 13·2 | + 20·85 | + 12·75 | + 7·25 | + 8·07 |
| May . . | + 44·1 | + 15·7 | + 21·38 | + 14·40 | + 10·05 | + 10·59 |
| June . . | + 47·9 | + 19·2 | + 25·48 | + 18·49 | + 13·11 | + 12·85 |
| July . . | + 50·8 | + 21·9 | + 27·30 | + 18·37 | + 14·59 | + 13·86 |
| August . | + 43·6 | + 16·4 | + 28·44 | + 19·95 | + 16·27 | + 15·01 |
| September . | + 39·0 | + 16·0 | + 22·55 | + 16·98 | + 15·16 | + 13·49 |
| October . | + 21·7 | + 4·8 | + 12·36 | + 9·93 | + 11·90 | + 8·81 |
| November . | + 18·1 | + 3·6 | + 6·79 | + 5·18 | + 7·51 | + 4·23 |
| December . | + 12·1 | + 1·6 | + 1·44 | + 0·57 | + 3·09 | + 0·03 |
| Mean . | + 31·75 | + 10·04 | + 15·58 | + 10·58 | + 9·03 | + 7·87* |

On the 16th of June, 1828, a thermometer in the soil during a west wind rose to the temperature 54° R., whilst that of the air was 20·5°.

This condition of the earth must influence plants according to their specific nature, and produce many peculiarities in the distribution of plants upon the surface of the earth. The limitation of plants to a larger

* The temperatures here are apparently marked according to Reaumur's scale.—Trans.

or smaller district may frequently have its origin in the facility with which the soil may be heated. A well-known expression amongst gardeners and farmers for a certain injurious peculiarity of the soil is "cold" ("kaltgründig"). The colour of the earth has a considerable influence on its power of absorbing heat. In Graziosa, one of the Canary Islands, Humboldt found close together some basaltic sands, which were coloured white and black; whilst the first had a temperature of 40° C., the last reached 54·2° C. In the experiments of Schübler, a mixture of various kinds of earth, in an atmosphere of 20° R., when covered with a white surface, afforded a temperature of from 33° to 34·8° R., and when with a black one, from 39·1° to 41° R. The same earths in their various natural colours, whilst in a dry state, varied in temperature from 28·1° to 31·8° R., and in a moist state, from 34·1° to 37·9° R. From these experiments it would appear that the chemical nature of the soil has but an extremely small influence upon its power of absorbing heat. As the dark colour of the soil almost entirely depends upon the mixture of organic matter, so we can see that the humus may thus exert an important influence on vegetation, without affording plants any of their nutriment. When we put together all the foregoing facts, in relation to humus, with this one, we can explain the strikingly favourable results of the action of humus, without in any manner regarding it as a nourishing substance.

§ 203. II. Heat, light, and electricity must be mentioned in connection with the assimilation of the absorbed nutritive matters. Without heat and light none of the important chemical processes in the plant can go on. A similar statement may, perhaps, be made concerning electricity; we are here, however, without positive proof from experiment.

Heat has been already spoken of; and in reference to light, only matters of fact should be spoken of, as an explanation of the phenomena is impossible, since we are deficient in a knowledge of light, or rather of the source from whence light proceeds — the rays of the sun. The chemical effects of the sunbeams on inorganic matter is seen in the decomposition and combination of various elements, affording evidence of a powerful agency, which can least of all be doubted in the organised world, where isomerism, polymerism, and similar relations, make the transition of one combination into another dependant on the slightest collision. The facts are too evident, and too generally known, for any doubt to be raised. The pale watery appearance which darkness produces in plants, and the quickness with which they become green by the operation of light*; the great difference in the matter which is formed in the plant during the presence or absence of light, as seen in the cauliflower, endive, and other cultivated plants, are well-known facts. In following the analysis of the general appearances into separate chemical operations we are not always very fortunate, and this is because we have been satisfied with guessing at random instead of observing and investigating. Until recently, it was generally allowed that chlorophyll was a sub-

* During this summer I allowed some Oats to germinate under a vessel of zinc till the buds were four inches long, when they appeared of a pale yellow colour. They were then cut down, carefully washed, dried in blotting-paper, and then placed upon white paper to be further dried in the sun. In six hours the plants were almost perfectly dried, but they had all become of a green colour.

stance rich in carbon, and that the process of becoming green was an active deoxidation, or fixing of the carbon. The first who investigated this subject was Mulder; he at once came to the conclusion that chlorophyll was a substance analogous to indigo, was rich in nitrogen, and that the process of greening depends on an oxidating influence. He also discovered that the changes of sugar, gum, starch, &c. into wax and fatty matters in the herbaceous parts of plants, furnish the oxygen for this oxidation. We find, therefore, chlorophyll combined with fatty and waxy matters. It is equally well-known, since De Saussure's experiments, that the fixing of the carbonic acid and the excretion of the oxygen in the plant are dependant on the influence of light.

I will call attention here to one point more, even at the hazard of putting weapons into the hands of enthusiasts about vital power, as I am persuaded that chemistry will not long leave the question unexplained. Throughout the vegetable world we find the development of colours depending on the action of light, and still, with few exceptions (perhaps indigo and some resinous colouring matters), the colouring matter of plants, after having been once developed, fades on being continuously exposed to strong light, especially if the colouring matter be separated from the entire plant. Thus chlorophyll and many of the colouring matters most intense in colour, chiefly reds and blues, instantly fade on being exposed to the light, as soon as they are separated from the plant.

Of the influence of electricity I shall say nothing, because as yet we know nothing.

## V. *Motion of the Sap through Plants.*

§ 204. All plants, from mosses upwards, distribute the absorbed fluid, by endosmosis from cell to cell, through the whole plant. Where there is the greatest evaporation, there is the greatest concentration of sap; where there is the greatest activity, through perhaps the change of thinner into thicker matter, there is the greatest endosmotic power. Hence the greatest stream of sap is directed to the green parts and the buds. This distribution or absorption is uniform in all tropical plants which vegetate continuously. With plants of other climates it varies periodically, according to the season. A point of time at length occurs when, in consequence of meteorological changes, the chemical activity and evaporation, as also the distribution and absorption of fluids, is almost entirely suspended. On the approach of a genial season they are again active. In what way the chemical activity, exhalation, and consequently absorption, is put in motion, in the torrid zone at the approach of rain, in the temperate zone at the approach of spring, is yet unknown to us. Yet in the temperate zone heat, and in the torrid zone moisture, appear to have the greatest share in the process. We must conclude, therefore, that they are the two principal conditions of the chemical processes. Even the phenomena of their renewal of vital activity are only known to us superficially. We only know thus much, that a great quantity of fluid is drawn up with great power, that the starch already

existing in the plant is changed into sugar and gum, and that with that change the development of the new leaves and buds takes place. In perennial dicotyledonous trees, it is followed by the formation of the new yearly rings. How the single cells assimilate their own sap, is only very generally determined in each species of plants: in the light, they form much mucus, chlorophyll, and bitter extractive (tannic acid); excluded from light, more gum, starch, and sugar. Definite compounds, according to the specific variety of the cells, and always as simple matters (volatile oils, fixed oils, gum, and jelly), are discharged into the intercellular passages, and form the very different kinds of milky juice seen in the milk-passages and milk-vessels. The process of this inward excretion is yet unknown.

Lastly, the following fact must be noticed: — All the fluids in particular cells (as in the pith and spiral vessels) are withdrawn, or the cells (as parent cells), or masses of cells (as those of the ovule), are through chemical processes dissolved, and this fluid is absorbed into the general masses of sap. This process, which is yet entirely unexplained, is called *Resorption.*

In Vegetable Physiology no part of the science is so much in its infancy as the study of the motion of the sap, because of the aimless and unsuitable experiments and analogies with which unhappy caprice has retarded the progress of the science for a century and a half. The oldest unprejudiced observers, Malpighi, Grew, &c., furnished with the necessary physical knowledge, observed that the spiral and porous vessels only contained air, and named the former *tracheæ.* Then came, at the beginning of the last century, Magnol, with the unlucky idea of putting parts of plants which had been cut off into coloured fluids, and therefrom drawing conclusions. That parts of plants which have been cut off take up fluid in their spiral and porous vessels, was made the foundation for all the idle theories that have been broached concerning the circulation of the sap in plants, and for the false analogies proposed between them and the higher animals. This resulted in the drawing up of a complete account of the motion of the sap, which had no foundation but in the imagination of its authors. The crude sap was conveyed by the woody bundles up into the leaves, where it was assimilated, and from thence was carried downwards into the bark, in order that the cambium might be separated, and the elongation of the roots effected. It is grievous to pass through the history and literature of the science, and to see with what nonsensical absurdity men spun in their heads fancies, which they endeavoured to prove to be actual facts. The greater part of this error depends on an almost entire neglect of fundamental microscopic investigation. But in recent times, with improved instruments and methods of investigation, prejudice is decreasing, and our efforts are encouraged and not overpowered. The most remarkable example of the kind is Treviranus: in his chapter on the vessels he says, most justly, "I have never, on examining the vessels immediately after their separation from the woody bundles, perceived in them any thing but air." He next gives the accurate observations of others, the striking testimony of Bernhardi and Bischoff, to the same facts: he appeals to the evidence of those whose only wish is to investigate cautiously. When speaking of the motion of the sap he, however,

almost entirely forgets the result of his own observations, and speaks of it as taking place in the vessels, as if it were unnecessary to bring forward proof of the fact. Link* evidently intends to bring forward some testimony which will be found nearly approaching to the truth, but he twice changes his views with regard to the contents of the vessels; I think, however, that he puts forth his views without having studied the subject sufficiently. A very clever observer, who bestowed eight days in the summer upon two hundred plants, in order to inquire into this subject completely, convinced himself of the fact, that plants in their perfectly formed spiral and porous vessels contain air only; therefore, when quickly brought under water and examined, they always appear dark. This holds good of our annual and perennial plants, and of the tropical ones, at least in our hothouses. The repetition of these experiments will convince every one, that no change of seasons, or time of day, brings about any alteration in this fact, except perhaps in some perennial dicotyledonous trees of our own climate during some weeks of the spring, and under especial and unnatural circumstances. Should this fact be once fully established, there is no further place for what the botanists in general say about the motion of sap, and a new course must be sought out. In what follows I divide the subject into two parts: first, the question concerning the absorption of the sap; and, secondly, the course which the sap takes through the plant.

On the subject of the absorption of the sap, people have used the unmeaning phrases, vital activity of the plant, vital attraction of the sap through the vessels, &c. Dutrochet first noticed the phenomenon of endosmosis, which gives a satisfactory explanation of the matter: no other explanation has at present been given. The conditions of the existence of endosmosis, namely, a fluid containing in solution gum, sugar, or albuminous (mucous) substances, separated from the water of the soil, impregnated with small particles of foreign substances, by membranes easily penetrated, are found to exist in all plants; so that, in order to ascertain the force with which the sap rises in the plant, it is necessary to observe carefully the process of the endosmosis. A solution of sugar of 1140 sp. gr., according to Dutrochet, caused the quicksilver in an endosmotic apparatus, during two days, to rise 45″ 9‴, exhibiting a pressure two and a half times greater than that of the atmosphere. In all the experiments of Hales, Meyen, Mirbel, &c. on the vine, the quicksilver never rose in so short a time above 15″. If it even be allowed that the sap ascends in the vessels as continuous tubes, there yet remains a superabundance of power for the endosmose. This is, however, not the case, and the endosmotic action is only exerted from cell to cell. In this manner the pressure of the fluid above upon the universally diffused endosmotic membranes is reduced to a minimum; and in the second place, it is not probable that its collective effect is thereby increased: but on this subject we have no experiments. There is here, however, a great range of problems to solve, as, besides the various endosmotic experiments in relation to the action of different kinds of endosmosis one upon another, there is the consideration of its effects observed in living plants, especially with regard to the contents of the cells, their specific gravity, their elementary constitution at different heights in the plant, &c. All this occurs in the rising of the spring sap in the trees of

* Wiegmann's Archiv, 1841, vol. ii. p. 278.

our climate. At all other seasons, and in other plants, endosmosis is assisted by evaporation through the leaves, and it is very probable that the passage of sap at these seasons of evaporation is stronger and quicker than that in the spring. Although much has been said on the subject, yet useful observations fail us. With regard to tropical plants, cultivated artificially in hothouses, they do not offer information of a kind that can be safely relied on. Many twining plants of the tropics, when cut through, allow much sap to exude, and Meyen therefore thinks that they are always to be found in the condition of our forest trees in the spring. I think that such an opinion is without foundation, and I wish that our governments, instead of sending out mere collectors of species, would send out some with the necessary authority and proper instruments into those countries where these phenomena are to be observed.

The second question is concerning the course of the sap in plants. The facts are as follow:—The so-called vessels in most plants never convey sap; and with others it is probable that they convey it only during a few weeks while the new buds are forming: where the greatest consumption of sap is going on, the vessels of the part are not found to contain it. In many important organs, where the vital processes of vegetation go on, and formative energy is present, as, for example, in the stamens and ovules, there are scarcely any vessels: large masses of parenchyma, in which thousands of cells lie close together, actively vegetating, contain no vessels: five great families of plants, namely, Algæ, Lichens, Fungi, Mosses, and Liverworts, have no trace of vessels; and amongst other plants several species have no vessels. After such premises, unprejudiced observers will hardly assume the motion of the sap through the vessels, or draw conclusions upon such a presumption. Nothing is more certain than that in most cases the nutritive fluid which the single cells need, must be taken up from other cells; and it is superfluous to imagine another mode of conduct of the sap for less frequent and less important cases. On the significance of the vessels, and the bundles of vessels, I have before spoken (§ 34.); and the conditions which they present, their origin and their form, appear to leave no doubt that they are the effect, and not the cause, of a living movement of the sap in a fixed direction. Where there is a considerable formative process and great chemical activity exhibited, the circumstances of a stronger endosmosis exist, and a greater stream of sap is afforded. This stream of sap acts upon the cells through which it passes agreeably to the laws of cell-life. The cells become changed into lengthened cells and vessels, and thus far allow the passing of the sap. For this reason vascular bundles are seen near every bud, and especially the most active developing terminal bud, and also near each developing leaf, &c. Where chemical activity is feeble there is no such active passage of sap, which shows that it exercises an important transforming influence in the cells. The originating cause at work in this case is the attractive power of the mixing heterogeneous fluids; but the possibility of the motion lies in the universal property of vegetable membrane of allowing fluids to pass,—the capacity of imbibition (§ 39.). I have already given, in my treatise on the Cacti, my views of this subject, and remarked that we need not seek any further explanation of how the fluid passes through the membranes, but rather why, in certain cases, it is held back. The reason thereof is partly that one side of the membrane is in contact with air which cannot escape, and which cannot be absorbed by the fluids contained in it, and partly that there are on each side of the membrane fluids which will not

mingle; as oil or resin on the one side, which will not mingle with watery fluids that may be on the other. Link (Wiegmann's Archiv, 1841) says, in reference to my view of the subject, "That as the inanimate membranes of plants resist absorption, as we daily see, so it is plain that this property was originally possessed by the living membrane." This conclusion was at least rash, for we know from chemistry that there are many substances that were once held dissolved in water, but which, when the moisture evaporates, will not dissolve again; so may a membrane which, when living, was permeable to fluid, lose that power when entirely dried. But it is to be regretted that Link did not pursue his investigations; as he had daily opportunities of doing so, he might have rendered important service to artificers in wood, who derive from chemistry their artificial varnishes and paints, by which they prevent the entrance of water into wood. I daily see that wood, linen, paper, &c. are penetrated through and through by fluids, that washed boards are wet to a considerable depth, that wooden vessels standing in water are penetrated by the fluid one quarter of an inch, that the boat-maker reckons on a certain loss in sunken wood, because, when saturated with water, it will lose all the air which, when swimming, it contained; hence, also, thick wood is longer in being saturated, because the air in the cells is longer escaping: this is daily experience. By scientific investigation we learn that vegetable membranes are as serviceable for endosmotic experiments as animal; that the starch in the cells of a slice of potato kept for a week is coloured by iodine, as in the fresh potato; that if old dead wood, pith, cotton, &c. be observed through a microscope, all the cells are filled with air, but as soon as a drop of water is dropped upon them the air will be absorbed and the water fill the cells. In short, the living and dead membranes show no difference: the former, because naturally containing more fluid, will absorb more quickly than the latter, which are entirely dry, and must be wetted before they absorb. All this Link might have known, and should have known, when he wrote upon the subject.

Yet with all this we have no evident movement of the sap in the plant. The watery sap in the cells is scarcely at all compressible; the cell-walls are so little elastic, that in the coherence of the entire plant they appear almost as fixed; expansion and contraction is so slight, that no observation gives us any intimation of it. It is quite different in animals, where, in the elasticity of the walls of the vessels and the motility of the contiguous soft parts, the conditions are afforded of locally or generally emptying or filling them. Fluid cannot, therefore, enter a cell (and consequently a plant) before room has been made for it by the escape of the fluid before contained in it. As, however, all cells are filled with fluid, evaporation alone can empty them. In the most important sense, therefore, is the motion of the sap in plants, as well as its presence, quantity, and direction, entirely dependant on evaporation. The greatest quantity of sap flows in the direction in which there is the greatest evaporation, which is constantly to the leaves and youngest parts. The motion of the sap, therefore, must be strongest where the plant has most evaporating organs: it is strongest in summer, because there is most evaporation; weakest in winter, because there is least. Together with evaporation is another condition (chemical change), which is, however, but imperfectly explained. By the change of the sap into solid or fluid compounds, the specific gravity will be generally increased; and by the diminution of volume room is made for the entrance of more

fluid. If, however, we observe the processes going forward at any particular instant during the whole time of vegetation, it will be easily seen how inconsiderable is the chemical process in the plant in comparison with the strong evaporation which is constantly carried forward. Evaporation assists endosmosis by means of suction. Little has been ascertained by botanists respecting this important question, because it is much easier to dream about a system at random than to observe, investigate, and experiment.

To the mind of a correct observer there can be no doubt that the fluid is not distributed regularly and normally through the vessels. A standing fact yet remains, which has puzzled most incorrect observers, namely, the spring sap. Most observations concerning the motion of the sap have been carried on in the spring on the grape-vine, and observers have pursued these experiments without considering plants in general. This is a perverted way of making observations. I am almost persuaded it will shortly be discovered that the spring sap, in the commonly received sense of the term, does not exist at all. In the mean time I would make the following observations:—It is generally known that if the branches of different woody plants, as Vines, Birches, Forest Beeches, &c. are cut, or if their stems are pierced in the spring, a large quantity of fluid escapes from the part with a power which corresponds, as in the vine, to the-pressure of more than two atmospheres. If the sap flows in a continuous stream, such a pressure (at least in vines whose old stems have vessels sometimes 0·3 *m.m.* (millimetre*) in diameter) must cause it to spirt out in a stream, which it never does; and this fact is entirely opposed to the idea of the motion of the sap in vessels. In the next place, the question is certainly to be answered,—Can we draw a general conclusion from the injured plant to the uninjured vegetating normal one? Plants which are not cut in the spring, as vines, never allow a drop of fluid to escape; they cover themselves with leaves neither earlier nor later than those which are cut,—as I this year observed, and as has been observed by Mr. Baumann, a botanical gardener of great experience. A vine-branch which measured 0·011 *m.* (metre*) in diameter, and extended in length along the ground 1·446 *m.*, with an almost horizontal elevation from the soil of about 0·2 *m*, delivered between 11 A.M. of the 25th of April†, and 5 P M of the 2d of May, 4550 C. Cent. (cubic centimetre*) of sap; therefore for the hour 30·33 CC. It was united with a glass tube by an India-rubber band, which was fastened into an alembic by a cork; another tube, drawn out fine at both ends, also went through the cork, and by this means possibly served to lessen the evaporation without making the escape of the air from the alembic impossible. With another branch B. (2·396 *m.* long and 0·10 *m.* thick, with a similar direction), I tied up the alembic with only an India-rubber gutter, somewhat open above, so that the air had free entrance to the cut surface. This branch gave out, during the first six hours, less sap than the other, and ceased to bleed much earlier. In the whole, I received from it 3220 CC., therefore for the hour 21·406 CC. of sap. That so great a stream of sap cannot have place in the uncut and naturally growing plant, is shown by the fact that such a mass of fluid can in no way escape through the dry and air-filled bark. I must say that I have not been able to convince myself of the

* A millimetre is ·03937 Eng. inch; and a metre is 39·3710 inches, and a centimetre .39371 inch.—TRANS.

† On the 10th and 11th of April, in the same garden, the vine, in a favourable situation, had begun to blossom, and ceased on the 2d and 3d of May.

presence of sap in the vessels of cut and bleeding branches; but granting they contain sap for a short time, yet, as it appeared to the latest and strictest observer, E. Brüke (Poggendorff's Ann. 1844), the sap passes only passively out of the neighbouring cells into the vessels. But can it be thus in the uninjured plant? I think not; for before the sap begins to ascend all the vessels are filled with air. What becomes of the air? Brüke says it escapes or is absorbed. Does it escape through the cicatrices of the leaves? But the cicatrices do not bleed; and it seems more than improbable that they should allow of an escape of air, for under a pressure of 2½ atmospheres they resist the escape of a fluid of the density of distilled water. That it is absorbed, is not less improbable. The air in vessels is rich in oxygen (Bischoff). In the Vine (not including the pith, which is filled with air) it is certain that the volume of vessels is equal to the volume of fluid in the cells. Pure water absorbed only 6·5 vol. per cent. of oxygen, and of nitrogen 4·2 vol. per cent.; fluids which hold in solution sugar, gum, &c., yet smaller quantities (Saussure). It is impossible, therefore, that the air contained in some vessels can be absorbed by the fluids contained in others. By the most careful observation, I have found uncut vines to contain only air in their vessels. I believe that I have now made it out to be at least probable, if not entirely proved, that the effects produced upon plants that have been cut or pierced in the spring are only pathological phenomena, and that conclusions from them cannot be drawn for uninjured vegetating plants: this, at least, appears to me, at all events after what has gone before, to be very near the truth. It is very probable that there may not exist any other than a rapid stream of spring sap in the uninjured plant, but it is certainly much more inconsiderable than the summer stream. A middling-sized sun-flower receives daily more than a pound of water (Hales). Its leaves have not certainly half the superficies which the leaves of the vine-branch had, on which I made my experiment in the summer. These branches gave out in the spring, at the time of their greatest bleeding, almost 189·48 CC., therefore about 0·508 lb. Now in summer, according to all correct observers, the vessels are filled with air, while at the same time the stream of sap is doubly stronger than when the cut vessels are bleeding in the spring, and consequently every possible condition of a normal motion of the sap in the vessels fails. The phenomenon of the assumed spring sap has misled observers.

The power with which, according to Hales and others, the fluid is poured from the cut branch exists also in the uninjured plant only as an endosmotic expansion of the extremity of the root, and is very probably greater in the spring than in the summer, because in the summer the sap in the cells is less concentrated, and contains less of the fluids of the soil, and plants at that season vary more in density than in the spring. If the stream of sap is more considerable in the summer than at other times of the year, the cause is that the evaporation is then larger in amount, thus creating space for the stream, and then absorbing it.

Now, after these preliminary observations, we must keep the following points in view:—

1. That as no vessels with continuous tubes exist in the plant, for absorbing and conveying fluid, so the possibility of the motion of the sap rests on the penetrability of the cellular membranes by fluids.

2. The moving power which effects the entrance of the sap into the plant, and into each single cell, is endosmosis, assisted by absorption in consequence of evaporation.

3. The principle of the activity of the sap-stream in plants is principally found in evaporation, and perhaps, in a slight degree, in the chemical processes, through which a voluminous fluid is reduced to a smaller quantity of solid matter.

4. Evaporation and the chemical process often determine the direction of the sap-stream. New fluid is drawn up only into those parts where the already existing fluids evaporate, or are subject to chemical changes.

5. There is no reason for supposing that there is a returning stream of sap, since cells that are already full can receive no more.

6. A stream of sap passes from the absorbing cells to those where the greatest chemical activity and the greatest evaporation is going on, and both of these are found united together in the youngest and extreme points of most *Phanerogamia.*

7. Annual plants wither from below upwards; perennial plants of our climate, in the chemical inactivity of winter, die also first from below; the motion of the sap of both, or, at least, of the active stream of the summer period, is terminated in such a manner, that the surplus sap retires into the youngest and extreme points, and from thence escapes. Annual plants carry naturally all their soluble matter into these external evaporating parts; consequently, a cultivated land will exhaust the soil more when the herbage is cut ripe, or nearly so, than when cut green, because in the latter case more than half the substances remain on the fields with the stubble. Not only have the ripe plants taken up from the soil double as much in their long period of vegetation, but the most important matters, alkalies and soluble phosphates, are not equally distributed in the plant, but are accumulated in those parts carried away at the harvest.

Each cell now assimilates the sap, which is a longer or shorter time entering, according to the nature of the cells, that is to say, according to the chemical process, which is regulated by their first origin; and each must give out again as much of its contents as it has taken up by endosmosis from other cells. The absorbed fluid is distributed through the whole plant as it is required, that is to say, according to the demands of the individual chemical processes. As water is continually exhaled by plants in proportion to the dryness, motion, and warmth of the air, so the sap becomes concentrated, and thus interrupts the endosmotic process towards the other cells; this action is continued naturally downwards towards the root, by which new watery and unassimilated fluids are absorbed. If this stream of crude sap is artificially interrupted in its course from below upwards, the sap in the upper part becomes more concentrated, and its organising power increased. This is the simple fact which lies at the foundation of all those phenomena which are brought forward to support the groundless hypothesis of a descending bark-sap. The two most important facts upon this subject are, 1. The magic ring (ringing fruit-trees), 2. The action of grafts. If from the circumference of a branch or tree a ring of bark be removed, the upper part will bear richer blossoms and fruit; the latter will ripen quicker, the leaves will be thrown off sooner, and the trunk will become thicker and stronger than in the part below the cutting. All this is completely explained by the foregoing facts, without making it in the least degree necessary to assume the motion of any descending proper juice or bark-sap, which certainly does not exist.* When an Apricot-graft grows from the trunk of a Plum-tree,

* The effects of ringing the bark remains the same if the branch be bent down, but not if it be turned back, as the ascending sap immediately enters; if the upper, instead

the latter is naturally and by degrees clothed with apricot-wood *; for out of the same soil an apricot-tree would merely take up the same crude sap as the plum-tree; but afterwards, in proportion as the leaves and branches of the plum-tree, or of the apricot, evaporate, assimilate, &c., plum or apricot-wood will remain. For these facts there is less apparent need of the fabulous bark-sap than in the former case. It is, indeed, unnecessary to treat of the various speculations, and on the especial motions of the bark-sap, or the causes of its motion, &c. A close microscopic investigation entirely suffices to show that in the parenchyma of the bark there does not exist any general matter capable of organisation, and that in the liber-cells, air, solid resinous matters, or milk-sap, are principally present. Nor is it worth the trouble to investigate the copious statements concerning the movements of the bark-sap, from the outer to the inner parts of the trunk through the medullary rays; nor to discuss, what is evidently so imaginary, that no one has experimented thereon or can do so. It is very evident, however, that the cells of the medullary rays generally have contents differing from those of the parenchyma of the bark, also from those of the liber.

I have already spoken of the meaning of the word "gland" with regard to plants. Here we touch on a subject connected with it, namely, the segregation of certain substances in an intercellular sap-passage, which in two ways require further explanation: 1. By what means so large a quantity of cells are destined to form gum, jelly, or oil, and to deposit them in their different canals; 2. The process of the secretion itself. It is a fact, that in this case the single cells have the same relations as though the walls of the intercellular spaces formed the outer surface of the plant; but the difficult point is the apparent impossibility of evaporation from sap-passages surrounded by water.

The complicated relations of the milk-sap to the neighbouring cells, from which it yet must be secreted, is still more doubtful to us, since we do not yet know the cause of the secretion, the manner of its origin, nor its relations to other cells, &c. (§ 319.)

I have now to speak of *resorption.* The fact is well known to every attentive observer, nothing needs to be added on this subject. Of the cause of the taking up of the fluid, especially in the spiral vessels, we are entirely ignorant. I have often used the word resorption when speaking of this circumstance. Link ridicules this, because there are no resorbing vessels in the plant, and thinks that I intended by this a fluidifying or organic melting (Wiegmann's Archiv, vol. ii. 1841.); this objection brings strongly to one's mind the obscure physiological notions of the last century. Coagulated blood, plastic exudations, cells, and masses of cellular tissue, must, through chemical processes, have first become fluid before they could be absorbed. In this process the absorbents (lymph-vessels) in animal bodies take no part, neither is the idea of resorption connected with them. It consists in a removal of the fluid from the place where it is deposited, and an absorption into the general mass of sap. Absorption cannot take place in invertebrate animals through the absorbing vessels, because they do not exist. It goes on even in vertebrate animals, as in the serous cavities, but not by means of the lymphatic

of the lower end is made to absorb, sufficient proof is afforded that no descending bark-sap exists. These facts are frequently used to support the theory, that the existence of a downward movement of the bark-sap, neither the movement nor the sap being demonstrable, is not dependant on gravity, but on a living vital power.

* Although universally thus stated, it is not the fact (§ 204.).

vessels, because the fluids are in immediate contact with cells, and can therefore only be taken up immediately by them: in this imbibition consists the very essence of resorption. Where the fluids are distributed by a vascular system, as in vertebrate animals, this happens also to the resorbed fluids; but if the distribution of fluids takes place from cell to cell in plants and invertebrate animals, so does the same take place with the resorbed juices; but this distribution of fluid is altogether distinct from resorption. The term, however, I think, is perfectly admissible, and without adopting it, a word would be wanting to designate a recognised important process in Vegetable Physiology. In using it, there is no occasion to think of processes going on in the animal system; and even then it is more correct than such a word as sex (*sexus*), or male and female, &c., words without any foundation, and only expressing foregone conclusions from Zoology to Botany.

## E. *Reproduction of Plants.*

§ 205. There are four conceivable ways in which any given plant may have originated.

1. From the spontaneous meeting of pure organic matters with a specifically-defined organic form.

2. From the spontaneous formation of a specifically-definite organic form out of formless organic matter.

3. From the development of a separate organised (cellular) formation from a definite species of plant.

4. From the development of a separate organised formation (embryo in the widest sense) from a definite species of plant to a plant of the same species.

The two first suppositions, the so-called primitive or first generation (*generatio originaria, spontanea, equivoca,* &c.), and the third, do not appear, so far as observation is concerned, to be admissible. The fourth is alone correct.

The question about spontaneous generation is very imperfectly understood, and the first and second questions are often confounded with each other, which is evidently a great mistake, as a plant may certainly be produced from already formed organic matter, without interfering with those laws of our planet which forbid the supposition of the generation of organic forms from inorganic matter. No evidence can be brought forward to show that inorganic matter, independent of an organism, can produce organic matter. What is now wanting in chemistry is the formation of such matters as those which are found to constitute the assimilated substances of plants from the inorganic elements.

Nothing can be more groundless than the assertion, that chemistry could never succeed in producing actually assimilated substances from inorganic matter. But the discussion of this possibility has been entirely fruitless.

The rejection of the other two origins of plants has another foundation, and relates to the understanding of that which we call a species in plants. On this point disputes alone, but no philosophically accurate definitions,

are possible, for which we have to await further explanation on many important points.

I must here return to what I have formerly said respecting the possibility of reproduction. The origin of every definite form is determined by the matter of which it consists, and the conditions under which it is formed. As the mathematical construction of the growth of forms is yet unknown, we ascribe it to the formative power of the earth as the unknown cause of the same, and call the complexity of the conditions, under which the same form arises each time, a specific formative power.

I must here refer to what I have before developed, with regard to the signification of the cell (§§ 14, 66.). The individual cell, if it vegetates and passes through all possible stages of cell life, may be defined as a vegetable form generally, yet it cannot be placed along with other simple plants as a definite species, and though not subscribing to the parallel drawn by Schwann between cells and crystals, yet in this rational exposition the possibility is pointed out, that natural science may be able one day to regard the cell as the necessary form of a normal condition of a permeable (assimilated organic) substance, just as the crystal is a necessary form of the inorganic substance. Then would all individual and simple cells originating and existing in organisms be but a definite organic crystallisation, and between them and the definite species of plants, that is, the collecting these organic crystals into a definite form, there remains a wide step, which entitles us to regard them as a class between crystals on the one side, and plants and animals on the other. This would, at all events, give them another and simpler morphological law, as well as plants and animals which are composed of them. If we inquire further concerning the characteristic signs of the conception "species" in organised beings, the following suggestions occur. The law of the specification is of subjective origin; the manner in which our ideas and abstractions are formed, is the reason why we must seek to embrace according to general signs, species, and genera as the objects of our intellectual activity; and we can never arrive at these conclusions by thinking on individual beings which are intuitively apprehended by the definite limits of time and space, and known by the "here." These subjective sources of the law of specification would be without signification for our philosophical natural knowledge, if nature did not confirm our subjective apprehension with an objective reality. This is seen in the simplest form in the specification of elementary bodies, by which bodies closely resembling each other are all distinguished, and through the thousand possible different aspects of individual substances never pass into, however near they may approach, one another. What endless variety of appearances individual elements, such as pure sulphur or pure carbon, exhibit, yet not a single modification of the properties of sulphur or carbon varies, so that the one or the other should ever be regarded as a transition to selenium or iron. In a similar manner, though certainly, on account of their complicated relations in time, not yet accurately comprehended by us, we find the laws of specification in crystallisation expressed. In this mathematical science lends its acute distinctions; but in organisation our comprehension fails, and only complicated inductions can make the law available. And yet there exists the unavoidable necessity of the impossibility of pursuing science without these laws. The individual is perishable, and consequently all which appertains to it is so also. Science depends on the permanence of its objects, and upon this its gradual development and actuality depends, as well as its com-

municability; and it would cease to be science, or capable of development, if it remained confined to individual men, or perished with them. We must, then, in this case, devise a plan by which we may make use of the previous consciousness to assist in the application of the law of specification.

The most acute definition of the idea of species is the following: "To one species belong all individuals which exhibit, independent of time and place, and under the same circumstances, precisely the same characters." It is, however, in only a few instances that we are able to apply this principle for the definition of a species, least of all in those organisms in which the conditions of existence are so multiplied and entangled, that we can seldom entirely comprehend all, and therefore never establish a perfect identity of circumstances.

We must here hold fast the importance of the history of development as the principle of Botany; only in this can we hope to find a notion of the species that can, in the course of time, afford a group of constant and similar characters; but this constancy must be observed in the plant generally, and not in the perishing individual, and must continue through many generations. Nothing can be held to be a species which does not originate in an individual of the same kind; and, therefore, nothing that originates in spontaneous generation can be held as a species of plant, although it may otherwise, as a natural body, find a specific distinction.

The determination whether a plant is a species or not, will long remain the most difficult problem in Botany. If we had the entire knowledge of plants, and the laws of their morphological development, at our command, we should then be able to make our distinctions upon fundamental differences which necessarily flow from the idea of the plant beginning from above and passing down, till, out of those known laws which lie at the limits of the comprehension of the individual, we arrive at the idea of the species. The solution of this question will yet long remain an impossibility. Every other definition of the species presents endless difficulties, which proceed from the nature of the plant. The independence of cell life, and the principle which lies at the basis of reproduction, present especial difficulties. As cell life is independent of the morphological combinations under which it appears; so can a form which is evidently only in the early stage of its development, endure for a long time, because the conditions of its entire development fail, and at last become very much complicated: hence this form may be found in a large number of individual cases as the entirely developed plant. Further, as the foundation of reproduction depends upon the capabilities of such cells to develope themselves according to the same morphological laws as belong to the whole plant, so may we have, in an earlier stage of development, an individual cell from the mass, which, although it may have the power, yet needs the circumstances to develope a perfect plant, and presents a less complete form; so that whole families of plants that for a time appear essential, yet consist of unessential forms. Suppose that caterpillars and maggots had the power of propagating themselves, and their power of developing themselves into perfect insects existed under conditions very rarely arising, would not these be cited, at least for a time, as a peculiar family in Zoology? Hence we may conclude, that the growth of forms is the governing principle in the vegetable world, and the invariable (essential) characters by which we define classes are necessarily of a morphological nature. But the em-

pirical apprehension of vegetable morphology is not yet completed; a morphological system of laws cannot be yet perfectly laid down; nevertheless, we can alone determine, by morphological laws, what are and what are not essential characters: thus we grope in the dark amidst our researches. The happy grasp of genius is our only guide. Where we have not long-continued observations, embracing thousands of individuals, as in long-cultivated plants, to lay an inductive foundation, it is mere child's play to endeavour to determine what is a species, a subspecies, or variety. But on such questions much time and paper have been wasted. It is, however, important for the progress of science that every form that presents itself, whether it be a species, a subspecies, or a variety, should be described in the most accurate manner possible, in order that it may assist in constituting the definitions of a more advanced science. Every definition of a species must, in individual cases, be without any possible application, and all disputes purposeless, where every one must acknowledge there can be no result, because we possess no laws of distinction.

It appears probable, that, with regard to single cells, they may not originate by means of an organic germ, but directly out of certain organic or formless matters, as the fermentation-fungus. This, then, can be regarded neither as a fungus nor as a definite species of plant, but as a kind of organic crystallisation. Whether there are other forms of the same kind, as the species of *Protococcus*, we must leave to time to develope.

This discussion was necessary for the right understanding of the facts; whether any one be pleased to call the origin of the fermentation-fungus *generatio equivoca* or not, is very immaterial, and discussion thereon would be foolish in the present condition of our knowledge. There remains only the fourth mode of origin as that which can be adopted for the scientific investigation of plants.

§ 206. The self-subsistence and power of reproduction of the cell is the foundation of the reproduction of plants. From this power can each single living vegetating (parenchymatous) cell (or group of such cells) from amongst the mass of a plant form new cells, which themselves again obey the same morphological laws as the original, and thus form a new plant. The real circumstances whereby a new cell may become self-subsistent, and form itself into a new plant, are very various. There are various kinds of reproduction in plants, and one in particular for the first division of plants, the *Angiosporæ*.

1. In the *Angiosporæ*, *Algæ*, Lichens, and *Fungi*, there are no morphologically definite parts of the plant. The entire specific formative power from which they proceed, is present and expressed in each single piece. Hence these plants propagate themselves by means of accidental or normal division. Each piece becomes a new individual. This accidental separation is frequent in Lichens (from the death or destruction of the centre), and in *Algæ* also. The normal division takes place, as far as I know, only in *Spirogyra* *, a genus of *Algæ*.

2. The above general law shows itself in the conjunction of

* Wiegmann's Archiv, 1839, vol. i. p. 286.

various unknown favouring circumstances in many of the cells of a living parenchyma (as of a leaf), in which a self-existent developing process takes place, from which a new plant may arise. This is observed in *Malaxis paludosa* *, *Ornithogalum thyrsoides* †, *Ranunculus bulbosus* ‡, *Scilla maritima* §, *Eucomis regia* ‖, *Hyacinthus orientalis.* ¶

3. Simple living vegetating cells separate themselves from the mass of the plant, as in the *soredia* of the Lichens (§ 86.), or rising upon the surface of the plant, form themselves into little small-celled bodies, and then separate themselves from it, as in Liverworts and Mosses (§§ 97, 100.), and from these cells and cellular bodies a new plant is developed.

4. In certain spots fallen or broken off leaves, when in or upon damp earth, or in water, there are developed regular buds, which, after the gradual destruction of the leaf, become self-existing plants. Thus it happens in the divided surfaces of the leaves of *Echeveria, Crassula, Citrus,* &c., or in the small excrescences of the leaves of *Cardamine pratensis.* **

5. After wounding the parts of plants, for example, the nerves of the leaves or the stems, after peculiar internal changes, producing similar conditions, buds will sometimes form on the edges of the wound or on these formations, as on the cracked nerves of *Gesneria,* on the edges of wounds in the trunks of trees, on the knotty excrescences of the wood (Masern † †), on the separated surfaces of the knob-shaped points of the root in *Tropæolum tricolorum, brachyceras, azureum, violæflorum.* ‡‡ When naturally or artificially separated from the mother-plant, these buds all form themselves into new plants.

6. Sometimes buds, and frequently knobs of various forms, are developed on uncertain, seldom definite spots, in leaves still connected with the plant, which, after the separation of the leaf from the plant, become independent plants, as in the notches on the edges of leaves in *Bryophyllum calycinum;* in the upper or the under side of many *Araceæ* and Ferns, and especially frequently in the angles of the nerves of the leaves.

7. In the axis of the embryo and stem-leaves, one or more buds are normally formed in definite forms, which, when separated from the plant, become new individuals.

* Henslow, Annales des Sc. Nat. vol. xxi. p. 103. [Cambr. Phil. Trans. vol. v. part i.]

† Poiteau, Ann. d. Sc. Nat. vol. xxv. p. 21.

‡ Dutrochet, Nouv. Ann. du Musée, 1835. p. 165; also Meyen, Physiologie, vol. iii. p. 47.

§ Guettard, Mem. s. diff. p. d. Sc. vol. i. p. 99; also Treviranus, Physiol. vol. ii. p. 624.

‖ Hedwig, Kl. Abh. vol. ii. p. 128; also Treviranus, op. cit.

¶ Meyen, loc. cit.

** Cassini, Journal de Physique, vol. lxxxii. p. 408. Münter, Bot. Zeitung, 1845.

†† We have no common name for these growths, which Dutrochet calls *embryo-buds* (Lindley, Introduction to Botany. 3d edit. p. 79.), and which I have called *abortive branches* (Annals of Nat. Hist. vol. v.). — Trans.

‡‡ Münter, Bot. Zeitung, 1845.

8. All plants form, in a normal manner, in morphologically distinct organs, cells, which are to become new and independent individuals. They are seen in the three forms of the process of development in the *Cryptogamia*, *Rhizocarpeæ*, and *Phanerogamia*, in which the reproductive cells are the spores and pollen granules.

The eight preceding kinds of reproduction resolve themselves into four classes: 1. Reproduction through corporeal division, and only occurring in the *Angiosporæ* (1.); 2. That peculiar to the *Angiosporæ* and rootless *Gymnosporæ*, that is, reproduction by single parenchyma cells (3.); 3. That of *Gymnosporæ*, proceeding from the formation of buds alone (2. 4. 5. 6. 7. — § 134.); 4. That which occurs in all plants presenting the formation of reproductive cells (8.).

If we maintain what has been said upon the reproduction of individual cells and the process of growth, it results therefrom that every mass of cellular tissue, under whatever form it presents itself, as also the entire plant, has its origin in an individual cell, through whose reproduction through many generations the cellular tissue is produced, and we have to determine for the various species in what relations the individual cells stand to the whole plant, and what circumstances it requires in order to develope a new individual. The less a plant exhibits morphologically definite forms, the less circumscribed is the formative tendency which holds the cells together in the entire plant; in consequence, the cell-life will be more independent, and the formative power will be more easily communicated to individual cells, which, as the result of their multiplication, are arranged in the loose outlines of the parent plant. Whilst, on the other hand, the more powerful the formative tendency is towards the independence of the elementary organs, the more manifold and peculiar are the forms in which the specific characters of a plant are displayed, and consequently more intense and permanent must the influence be which the entire plant exerts upon individual cells and their development into new plants: hence these remain perfectly under the dominion of the same formative tendency, and are a true impression of its type. Therefore, in the simplest plants, as the *Protococcus viridis*, which only in their elementary organs can be regarded as a species, every formation of a new cell is an act of reproduction, and the new cell requires, in order for the species to remain true, nothing more than the unencumbered development of the universal cell life. In the constantly indefinite forms of the *Angiosporæ* (in which, however, the individual life of the cell is brought under an unvarying formative energy), reproduction is divided into two kinds, one from the mass of the cells, the other from a single cell, each originating under a definite form of the processes of formation, and serving exclusively and necessarily for reproduction. We find a continuous series from the almost entire identity of both processes (in the formation of a special cell) in the simplest *Algæ*, even to one of the customary reproduction of the cell through the peculiar phenomena of essentially varied generation of the definite reproductive cells in the Lichens. In the Mosses and Liverworts, the formative tendency exhibits a more strict and limited conformity to law, as is seen in the presence of an axis and leaves, and in the more complicated forms of the remaining organs. Here ceases the first kind of reproduction, in which a single cell, withdrawn from the mass constituting the individu-

ality of the whole plant, is able to produce a new plant. The isolated cell must first stand in relation with the parent plant, and come under the dominion of its specific formative tendency up to a certain point, before it can be placed in circumstances to introduce the same law of formative tendency into a new independent life. It is formed into a little cellular corpuscle which is separated from the parent plant, as in *Mnium androgynum*, *Marchantia polymorpha*, &c. From this point and upwards ceases in the vegetable world the process of reproduction through the separation of cells, and in its place commences the formation of buds. And here we arrive at an entirely unoccupied void in our researches, which is filled up with mere hypothesis. Analogy allows us the following conjectures: — A parenchymatous cell, through the growth of new cells, without becoming isolated upon the surface of the plant, becomes the occasion of the origin of a mass of cellular tissue, which is in close union with the plant, and scarcely to be distinguished from the surrounding parenchyma, but at the same time it already represents a special individuality, but as it originates entirely under the influence of the specific formative tendency of the whole plant, it subsequently becomes essentially independent of the parent plant, forms the foundation of a plant with axis and leaf — in a word, becomes a *bud*. To what parts of the plant the first cell belonged is indifferent; and according to all possible varieties are the circumstances various which determine the development of the cell to the plant. In the axis of the leaves these circumstances are always normally present, at the basis of the leaves frequently, on the surface of the leaves and the ligneous axis seldom, less frequent still on the herbaceous (annual) axis, and least frequent of all on the parts of the flower. At the present we have no accurate researches upon the formative processes which precede the elevation of the bud upon the surface of the plant, and it would be only through an accurate knowledge of the same that we should be in a position to determine whether the facts are as I have above conjecturally stated or otherwise.

We must now follow another series, the development of the definite reproductive cells (spores and pollen-grains) which are normally formed for the development of the new plant. In the simplest *Algæ*, as before remarked, this process is scarcely to be distinguished. In the simplest way a plant cell forms a filial cell (Brut-zelle), which after the destruction of its parent cell becomes isolated, and is developed into a new plant. In the remaining *Angiosporæ*, the process of growth in the reproductive is connected with a peculiar law, which exerts a special influence upon its nature. In the Lichens are first seen definite indications of a peculiar layer of separation which surrounds the reproductive cells, and it is not improbable that it may preserve them from those external agents which, upon the form of the process of development, could exert any influence. In this also a new circumstance is seen, which is afterwards found in all classes with the exception of plants flowering under water. In the *Rhizocarpeæ*, however, the reproductive cell (spore), without further development, proceeds from the mass of the plant and forms a new individual; but from the Mosses upwards we find that the origin of the same is connected with a definite morphological law, and constantly originates in a determinate independence of the specific formative tendency, and is exclusively connected with the formation of the leaf. But in the *Rhizocarpeæ* a new stage sets in, not only the formation of the reproductive cell, but the first development

of it under the influence of the parent plant and its specific formative tendency. Of this we have two phases in the *Rhizocarpeæ* and *Phanerogamia:* in the first, the influence exerted upon the development of the pollen is mediate, as the seed-bud (ovule) is separated from the parent plant; in the *Phanerogamia*, on the other hand, it remains in living union, whereby the developing new plant continues longer and more entirely independent of the specific formative tendency of the parent plant. Thus we see how the specific formative tendency encloses the organism within constantly narrower limits of law, and also how the circumstances of the parent plant under which the reproductive cell must develope become more complicated, and thus communicate to it a similar morphological development, and make it, as a new individual, to represent the same formative tendencies as the parent plant.

In the paragraph I have arranged the various modes of increase of plants, according to the most general point of view, under four heads. These may be subordinated again as follows: —

*A.* Immediately that every part of a plant is formed according to one and the same principle of development, every part of the entire plant is capable, through simple division of the plant, of producing a new independent individual. This is *increase of plants by division.*

*B.* But if in the plant the law of development exhibits an essentially different kind of phenomenon, so that a part of a plant is not developed into the entire plant, but receives the impression of the entire law of development, then is the growth of the whole plant from a part impossible. This occurs in the simple plants among the *Gymnosporæ*, in which the axis and the leaf, as two different processes of development, belong to the idea of the whole plant. In this case the plants increase in the same way as an elementary part; a single cell would increase through the special properties that were communicated to it. This same process, together with accidental division, is normally present in the *Angiosporæ;* and this process, in opposition to that of division, is called *reproduction*, and is found present in all plants. But this reproduction presents itself under two phases, as we have before observed: —

*a.* In the development of any living cell to a new individual under very various circumstances = *irregular reproduction.*

*b.* In the development of a special reproductive cell, exclusively developed for this purpose = *regular reproduction.* This divides itself into two, according to the circumstances under which the reproductive cell is developed: —

1. The origin of the reproductive cell, independently of the parent plant = *asexual reproduction*, as in the *Cryptogamia.*

2. The development of the reproductive cell to a new individual under the circumstance of a material influence of the parent plant. This last we call *sexual reproduction;* it is present in *Rhizocarpeæ* and *Phanerogamia.* This, and only this, is the signification of the word sex amongst plants, and all comparisons with the higher animals are lame and unscientific. We need an expression for these conditions in the vegetable kingdom, and I would, with Valentin, banish the word sex, if it were not to be feared that those who are not free from ignorant prejudices would, with the abandonment of the word in the one kingdom, seek to do the same in the other. If we divide the word sex into two, male and female, we must, according to analogy with the animals to which the words are applied, call those organs female in which lie the material organised (cellular) foundation which subsequently becomes the new individual. If, then, we apply the

terms to the *Rhizocarpeæ* and the *Phanerogamia*, we must call the vesicle (sac of the embryo) which receives the pollen-grain the male, and the anther the female organ.

Of the utmost importance, and a problem yet to be solved, is the perfect history of the development of the bud from the individual cell, or group of cells, in which it has its origin. For this purpose the axillary buds can hardly be employed, as they are developed so early, that the cellular tissue itself, in which they originate, would throw great difficulties in the way. The buds of *Bryophyllum calycinum* and the adventitious buds of stems (which may be artificially produced) seem to offer a means of solving this problem by very careful research.

§ 207. Every formative effort, especially in the organic world, establishes the possibility that some characters of the individuals which we regard as unessential, and yet falling under the idea of species, may vary within certain limits. The determination of essential and non-essential characters can only be arrived at when we shall know the construction of all the processes of formation. It has been heretofore supposed, that only regular reproduction could bring forth the essential characters of the individual, and irregular reproduction the unessential. This is entirely false; it depends on the peculiarities of individual plants, how far they are changeable in their characters in general, and how far they have a tendency to produce, through reproduction, unessential characters in the new individual. The general rule might perhaps be thus expressed: the longer and the more intimately the newly-developing plant has been in connection with the parent plant, the more will the formative energy impress upon it both its essential and non-essential characters. Hence, with reference to the several kinds of increase, we come to the conclusion, that, under generally similar circumstances, plants grown by division or from buds will closely resemble the parent plant in all their characters; buds, the more closely, the further their development had proceeded in connection with the parent plant; and in regular reproduction, the farther that the embryo has been developed under the influence of the parent plant, the more like to it will be the characters of the plant which is produced from it.

Lastly, it is to be remarked, with respect to the *Phanerogamia*, *Rhizocarpeæ*, and some *Agamia* provided with roots, that the bud, when organically united on one side with the parent plant, never developes a true root, but an adventitious root.

Physiology, and we may almost add Botany, has paid attention entirely to the *Phanerogamia* rather than to plants in general; the remaining plants have been grievously neglected, or treated in an off-hand way, according to false analogies. Hence we find in the old systems that the function of reproduction has been almost exclusively regarded, from the cases most easily observed, as increase by means of either seeds or buds. The foregoing paragraphs will have shown how unjustly circumscribed is this view. Connected with this subject, we must allude to a point which even the superficial observation of the seed and bud suggests. We often find it asserted, "The seed repro-

duces the species; the bud the individual." The instruction of our early days in the Latin and Greek languages has taught us that the German philosophers understand nothing less than their own mother-tongue; and this is seen in this case. The organic increase of an individual is termed growth. When by an organic process, conducted under given conditions, a new individual arises from the old one, the plant has been reproduced, or propagated. Species is an idea which, in the abstract, cannot propagate or be propagated, reproduce or be reproduced. If through reproduction one individual existence arises out of another, thus the idea of species is applied explanatorily, because the concrete objects are present that fall within its sphere. Link imagined that he was improving upon the above, when he said, "The seed continues the species, and the bud the individual."* I cannot conceive of the Creator as a journalist, who issues his works leaf by leaf in continuation. Science regards a tree as an aggregate of many individuals, a kind of polyp-stock; life, proceeding upon another distinctive character, calls it an individual: but neither science nor life as $\frac{1}{1000}$th of an individual. I imagine that any person of sound mind would smile if any one were to regard the 2000 poplars of a German chaussée a mile in length as a continuous individual; and still less would it be admitted, that a one-year-old span-long shoot of a weeping willow was essentially a continuation of an old individual, who, in his rapid departure from the East, left his youth lying on the border of the Euphrates, where long ago it died and was decomposed, whilst its commencing manhood was cherished by Alexander Pope†, and many years since was hewn down and cast into the fire. The above facts, which the want of observation and a knowledge of the mother-tongue have rendered so confused, are, that from buds originate individuals, which frequently resemble the parent plants in more characters than those which originate with the embryo. This fact, but which in no way constitutes an accurate distinction (as seen in the subordinate characters of our common garden vegetables, cabbages, peas, &c., which are produced from seed), bears very naturally on the species produced generally by organic reproduction. Reproduction is nothing else than the passing over of the specific formative tendency of one individual to a new one; and where the species is not maintained, there no reproduction can take place. But the circumstances under which reproduction takes place determine whether the specific formative energy shall produce a larger or smaller number of characters; as a form in a condition of development, whether it consists in external shape or internal process, must become more like the earlier form, the longer and more exclusively its origin and development depend upon those circumstances which produced and developed the first form. Regular reproduction, and reproduction through single cells, consist in the fact, that an organic embryo separates itself perfectly from the mass of the plant and its continuity, and developes itself out of itself, so that the influence which the parent plant exerts, even though it be definite and assimilative, is yet always an external one, and is modified by the peculiar vital power of the reproductive cell. In propagation by division and bud-formation, on the other hand, the new individual, up to the

* Elem. Phil. Bot. ed. 2. vol. i. p. 133.

† All our weeping willows in Europe have proceeded from a branch, which formed part of a wicker basket, which was sent from Smyrna to the poet Pope, and which he planted, as it showed signs of life.

moment of its separation, is in organic connection with the parent plant; its continuity is the same, and it is developed entirely under the formative tendency of the parent individual, with all the accidental conditions to which it is exposed. But that it can be influenced by many things independent of the parent plant, is proved by many cases. The so-called water-shoots (individuals developed from buds) are frequently distinguished from the parent plant by an enormous development of the leaves. Shoots of the oak, springing from a felled branch, are often found in woods with leaves a foot long. Grafts and eyes frequently become modified in their growth, and in no way possess the characters of their parent plants.*

§ 208. The various modes of reproduction are subservient in nature to the increase of individuals upon the surface of the earth. In many plants it is constantly present, in others it is only produced by extraordinary external agencies; and hence it occurs less frequently. There are many plants which produce a quantity of buds in various forms (§ 136.), which subsequently, through the death of the parent plant, or of the connecting internodes, become isolated. They are called *proliferous* plants.

Many horticultural operations, which have for their object sometimes the increase and the preservation and alteration of the plant, are founded upon the formation of buds.

The formation of buds on leaves, and the natural growth of buds, are both very generally used for the increase of plants. In the last instance, what are called *layers* are formed, in which a branch, whilst still attached to the parent plant, is placed in the ground, and the buds are allowed to put forth adventitious roots, and is subsequently cut away; or the branch is at once taken away from the parent plant, and allowed to put forth adventitious roots; such branches are called *cuttings*.

For the attainment of certain special objects in the culture of plants, buds are conveyed from one individual to another. This operation consists essentially in the bringing into close contact the exposed, living, vegetating, and similarly constituted cellular tissue of two plants, and then protecting it from external injuries till the two wounded surfaces are grown together. Thus buds are translated (grafted, inoculated), and are removed singly from the parent plant with a piece of the bark (eyes), or young branches (grafts), and are inserted upon stems (stocks) variously cut to receive them: the first are inserted under a loosened portion of the bark; the last between the bark and the wood, or are placed in contact with the stem, cut in a suitable manner. Another mode is, binding together the cut surfaces of the branches of two plants, and separating the one wished from the parent plant when the two have grown together. This process is called *inarching*.

I insert this paragraph, without having much more to say; for the first point belongs to Special Botany, and the second belongs as little to

* Lindley, Theory of Horticulture. London, 1840. p. 220.

Botany as Surgery does to Zoology. On the union of two individuals, however, through eyes, grafts, or inarching, I have a few words to say. Independent of the care which should be taken in this operation to bring in contact living cell-tissue and, as much as possible, similar tissue, as wood with wood, alburnum with alburnum, cambium with cambium, and to avoid the access of air, yet the success of this operation entirely depends on the species of plants which are thus united. The rule is, that the nearer plants stand to each other, as the varieties of a genus, the more certain will be the result. Plants belonging to different natural families will not unite. The exceptions are only apparent. A twig will blossom and form leaves in water or moist sand, and so it will in the moist tissue of another plant; but it will not grow together with the other, unless the chemical processes in both plants are similar. Did we know the specific peculiarities of the chemical processes in all plants, then we might *à priori* determine the results of such transference, and need not to perform the experiment. So soon as the union is effected, the nature of the future-formed cells and organs depends principally on the nature of the new individual, that is to say, when it is the only growing portion on the stock. Yet the stock must always exert a greater or less influence on the eye or graft, as the sap brought to it must pass through the cells of the stock, and become changed there. In this case the relations are too complicated to enable us to offer an explanation. All that is known on the subject is detailed in manuals of horticulture. I will mention one case. If a branch of a quick-growing plant is grafted upon a very slow-growing one, as, for instance, the branch of a plum upon a sloe-stock, the graft will grow rapidly, but not so the stock, which retains its slow-growing character*, — a striking example of the permanency of the specific life of the stock, and, as it appears to me, affording a fatal argument against the pretended descent of the sap. If a descending bark-sap existed, the sloe-stock would be naturally covered with annual rings of plum-wood from the graft, and it would grow in proportion to the growth of the graft; but this is by no means the case, for the new annual rings are formed, not out of a descending bark-sap, but out of a cell development of the cambium already existing in the stock, and having essentially the same characters. The formation of new wood of the nature of the graft has always been taken for granted, in order to prove the descent of the bark-sap; but we find that this wood does not partake of the nature of the graft, and that it must therefore be formed independently of any descending juices.

§ 209. Peculiar relations are exhibited sometimes in the capacity of plants for regular reproduction. Every simple plant, in the most stringent sense of the word, is only capable of propagation once; with the unfolding of its terminal bud into reproductive organs, its life is closed. But even the greatest part of the simple plants, in a wide sense, whose axillary buds are exclusively developed into flowers, are only once capable of reproduction; the plant is so exhausted through the reproductive effort, that it dies. This is the case with annual and biennial plants (*plantæ monocarpicæ*). Sometimes they continue to live, and the terminal bud

* Lindley: A theory of Horticulture, p. 237.

goes on developing, and is capable of producing new reproductive organs, as in *Ananas*. In compound plants, the same takes place with the single individuals of which they are composed. In this case a very remarkable condition sometimes occurs; the seed of many perennial plants, originating themselves from seed, is entirely incapable of reproducing the individual, and this power of producing reproductive organs is first possessed by buds produced from individuals in the tenth or more generation.

In the majority of *Algæ* and Lichens, in which we can hardly speak of a special individuality, and in which the smallest portion of the whole plant represents and lives for itself, the above law finds no application: on the other hand, it is more applicable to the remaining Lichens and to the majority of *Fungi*, in which the whole plant seems to consist of reproductive organs. In the rest of the vegetable world, it is understood that the individual proceeding from a bud, if its shoot is single and terminal, and is converted into reproductive organs, must die. The same must take place in the simple plant, whose lateral buds are all converted into flowers or flower-stalk, as soon as the terminal buds are converted into flowers. If the last does not take place, it depends upon specific peculiarity,—whether the life of the entire individual is exhausted in the formation of flowers (as in *Musa*, and some palms), or whether it continues to grow with a terminal shoot, which frequently produces reproductive organs (as in most Palms).

The most remarkable condition is that last mentioned, which takes place in most dicotyledonous trees. In this case the individuals which are produced very late from the lateral buds form reproductive organs. Perhaps there may be polypes placed in a similar condition, so that an animal developed from an egg is not in a position to form eggs, but that one of its lateral branches subsequently acquires this power.

### F. *Death of the entire Plant.*

§ 210. The life of the entire plant through the self-existence of the elementary organs exists as such only in the morphological union of the cells, and, as the plant never possesses all its organs at the same time, in the history of its development. It is thus that plants die immediately that there is no longer any possibility of individual development. If we distinguish plants into simple and compound, we shall find that only in a small part of the simple plant a termination of its process of development, and through this alone its death is determined; that is in the simple plant, whose terminal buds are developed into reproductive organs. In some other plants, it appears that, without any such development of the terminal buds, the vegetative power of the plant becomes exhausted through the development of all the axillary buds into reproductive organs, flowers and flower-stalks; but in what way we know not. In all compound plants, and in many simple ones, a special condition occurs in which the simple plant, as such, dies; but in one part, which is quite unable to develope new organs, it

continues to live. This living part then maintains in a peculiar manner a union amongst the new individuals (single plants), which are produced by formation of buds from the first individual. This is the condition of all perennial plants with root-stocks and stems. Perfectly simple plants, which entirely die after having completed their regular development, are extremely few. Compound plants have no determinate conclusion to their life which can be called death in the above sense of the word.

I have frequently pointed out in this book how irrelevant and useless all analogies between the animal and vegetable kingdoms are, so soon as we regard them without prejudice, and compare them, with a profound knowledge of the nature of each. This is seen in a remarkable manner in the subject of the foregoing paragraph. Not a hundredth part of the vegetable kingdom (the annual and biennial plants) afford the possibility of any comparison between the death of plants and the majority of animals. Not a thousandth part of the animal kingdom (the compound polyps) permits of an analogy with the remaining plants*; and our knowledge of the history of the development of these animals is most defective. The life of the individual animal is dependant, both for its stimulus and maintenance, in a manifold manner, upon the life of the planets [meteorological phenomena]. But whilst external nature supports the life of the animal on the one side, yet every act of maintenance is attended with a wearing and resistance which gradually culminates till the maintaining power is overcome, and death takes place. The conditions of death lie in the organism itself of the animal. The organic elements united to an independent individuality have no life for themselves, only so long as they serve for the life of the entire animal, and the specific determinate equilibrium of their chemical nature and physical power are maintained. The destruction of this equilibrium by external nature, however, is always opposed by a specific determinate *vis inertiæ*. When the event occurs which produces a perfect destruction of this equilibrium, then the death of the animal takes place; at the same time, all the organic elements of which it is composed fall under the influence of death and decomposition.

It is not so with the plant. In it each elementary organ has its own independent life, and dies for itself alone, and the entire plant consists of a morphological and not a physiological union of elements. Individual cells may die, although they give the figure of the entire plant, and yet a portion of the whole remain living; the entire plant may die, that is, the specific form in which the cells are arranged may be abolished, and yet the life of the elementary organs continue, and even be in a condition to produce again new individuals of the same species. The idea of the whole plant, as I have in so many places pointed out, consists in a specifically determinate process of development. Where this produces such indeterminate forms as *Algæ*, Lichens, *Fungi*, we cannot speak of the death of the entire plant, because every individual part represents the whole plant, and is capable of growth according to the same type. We

* An interesting relation between the morphology of plants and certain zoophytes was established by Professor Edward Forbes, in a Paper read at the meeting of the British Association for the Advancement of Science in 1844, entitled, "On the Morphology of the Reproductive System of Sertularian Zoophytes, and its analogy with that of Flowering Plants."— Trans.

can in this case only speak of death, when all the elementary organs are chemically or mechanically destroyed. On the great Fucus bank of Corvo and Flores we might yet find, floating about, plants of *Sargassum* which had been cut into strips by the bark of Columbus; and in the northern drift we might expect to discover Lichens that had been transported, with the soil in which they grew, from Scandinavia. On the primitive rocks we may find frequently examples of Lichens which, from a knowledge of their slow growth, we might regard as at least a thousand years old. The majority of the *Fungi*, on account of the delicacy of their tissue, are more easily destroyed, especially through decomposition, than other plants, so that we can hardly say that they die a natural death. Amongst high trees we often find the so-called magic circles, formed by *Boletus bovinus*, *B. edulis*, &c., having so great a circumference that the plant to which their spore-fruits (sporocarpia) belonged could not be less than from ten to twenty years old, the solid *Polyporus igniarius*, *Dædalea quercina*, &c., must frequently reach an age of above a century before they, Dryas-like, fall to the ground, which they do not because they are dead, but because the dwelling-place with which a hard fate has united them can no longer exist.

The fact is otherwise in the remaining groups of plants, which, by a definite modification of the process of development, form various organs essential to the idea of their existence. One of these plants can be said to exist only so long as it continues to form organs necessary to the idea of its existence. The occurrence of any thing to render it impossible to develope itself according to its peculiar law is the death of the plant. Hence the importance of the distinction earlier pointed out between simple and compound plants. As the existence of the latter does not depend upon the growth of an individual existence, but upon the continual reproduction and formation of new individuals, we cannot speak of their death, because we know of no necessity in organisms capable of reproduction that would induce in any one generation the cessation of the reproductive power. There exist no observations to prove that, under perfectly favourable circumstances, any tree ever died from the weakness of old age. On the other hand, we have examples without number of trees of prodigious age. The celebrated *Castagna dei cento cavalli* (*Castanea vesca*) on Ætna must be a thousand years old at least. The Baobab trees (*Adansonia digitata*) of the Green Cape demand of us, according to their thickness and the number of zones in some of their branches, an age of 4000 years, or thereabout. The gigantic cypress (*Cupressus disticha*) at Santa Maria del Tule, six miles east of Oaxaca, in Mexico, has a circumference of 124 Spanish feet, about 40′ in diameter. Now, suppose that every annual zone measured 1‴, the tree must be nearly 3000 years old. It is historically certain that it is older than the conquest of Mexico by the Spaniards. The age of the great Dragon tree (*Dracæna Draco*) at Orotava, in Teneriffe, is supposed to be 5000 years; so that, according to the ordinary calculation of the Hebrew chronology, it was a witness of the first creation. These examples* are quite sufficient to prove the possibility of a compound plant living on without end. These plants die ordinarily in consequence of mechanical injuries. A storm breaks off a branch, the broken surface is exposed to the action of rain-water; putrefaction or decay takes place, the firmness of the cell-tissue of the heart-wood becomes affected; and a

* There is a catalogue of old trees in the Appendix.

new storm casts the whole tree to the ground, separates the trunk from the roots, and it perishes of hunger.

In all the perennial plants there is a peculiar condition to be observed which is connected with reproduction, and which has before been mentioned. In the simple plant a mass of cellular tissue is formed which maintains a connection between the new individuals originating in the formation of buds, and thus renders possible the existence of a compound plant. In this way, individuals originating from seeds remain either living, and continue to grow on, as is the case in most trees, or the plant dies completely down, and leaves behind it only these masses of cellular tissue which, although living, are incapable of individual development, as is the case in undershrubs. In trees this mass of cellular tissue is the cambium of the stem ; in undershrubs it is that of the rootstock.

In the remaining (simple) plants we see thus much, that a plant whose terminal bud is completely changed into reproductive organs must have reached the end of its life, and cannot continue to grow. How it is that death occurs in simple plants, which only develope their lateral buds into flowers, is not yet understood. There is a negative explanation, which is, that it depends on an exhaustion of the vital powers through the development of the flowers ; but, as we have no definite conception of what these particular vital powers are, we can hardly regard this as an explanation. Much more must be done before we can draw correct conclusions.

I know of no book, whether on Vegetable Physiology or on Botany in general, in which the question of the death of the plant is more than incidentally mentioned. Unger and Endlicher have given a chapter on the subject in their "Grundzüge," which was published after my own observations, and contains similar remarks.

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## SECTION II.

### SPECIAL PHENOMENA IN THE LIFE OF THE ENTIRE PLANT.

### A. *Development of Heat.*

§ 211. The temperature of the living plant scarcely ever corresponds with that of the surrounding atmosphere.

The following three relations have hitherto been observed : —

*A.* Germinating seeds (of the *Phanerogamia*) develope a heat which considerably exceeds that of the surrounding atmosphere. This is most probably owing to the process of combustion in the formation of carbonic acid and water during the decomposition of the assimilated matters, starch, oil, &c.

*B.* Trees of our climate exhibit in their interior a variable temperature, being higher in the winter and lower in the summer than that of the surrounding atmosphere. These changes are always strictly in accordance with the changes of the atmosphere in their

rise and fall; if these conditions are of long duration, the temperature of the tree continually approximates more and more towards them, without, however, entirely reaching their degree of intensity. The reason of this phenomenon may, in all probability, be attributed to the temperature of the earth at the depths to which the roots extend; the temperature is thence imparted to the stem, partly by means of the rising sap, and partly also through the great capacity of conducting heat possessed by the wood in its longitudinal direction; and it is protected and preserved in the stem, partly owing to the inferior conducting power possessed by the wood in its transverse direction, and partly also owing to the bark, which is itself a very bad conductor of heat.

*C.* The *Araceæ* (in which the effect is more readily traceable, owing to the number of flowers aggregated together) develope, during their period of flowering, a temperature far exceeding that of the surrounding atmosphere. The reason of this is also to be attributed to the formation of carbonic acid (a process of combustion), which is especially maintained by the stamens.

Respecting the subjects touched upon in this and the following paragraphs of the general Organology, I must confine myself to reference to the labours of others, indicating the problems that are still to be solved, as I have not yet been enabled to institute observations of my own.

Every one who knows any thing of malting for the purposes of brewing must be acquainted with the rise of temperature that takes place during the germinating process of the plants. This fact is beyond dispute; but I am not aware of any scientific observations on the subject. They ought to be instituted in such a manner as to embrace the entire act of germination up to the cessation of the formation of carbonic acid; during this period the entire quantity of carbonic acid, as well as the quantity formed during the individual periods, ought also to be ascertained; the quantity of water formed ought also to be calculated according to the well-known composition of the starch, and the temperature generated from both through the chemical changes should be determined, and be compared with the temperature observed.

Observations respecting the temperature of trees were first instituted by John Hunter, subsequently repeated by many with different results; and animated controversies were carried on upon the subject, of which Meyen* gives an elaborate account.

All former investigations, however, appear to me to be superfluous after the observations of Schübler†, the first that were accurate and instituted in a scientific spirit. These researches resulted in the law enunciated in the text. The derivation of it from the temperature of the earth is still hypothetical, and accurate observations on certain plants, with simultaneous observations on the temperature of the earth at about the depth of the roots, are much to be desired. It becomes however very probable, after the known facts of the course of the temperature, of the

* Physiologie, vol. ii. p. 164.

† Halder, Beobachtungen über die Temperatur der Vegetabilien, Tübingen, 1826; and Neuffer, Untersuchungen über die Temperaturver nderungen der Vegetabilien, &c. Tübingen, 1829.

rise of the sap in the plant, and from the discoveries of De la Rive and Alph. DeCandolle *, from which it appears that wood in its longitudinal direction is a good, but across its fibres a very bad, conductor of heat. It is especially necessary that a greater number of comparative observations should be made; first, in plants the roots of which attain different depths; then in herbaceous and woody plants; and, finally, in tropical plants, which latter we shall probably be only able to obtain when governments begin to send out naturalists instead of collectors for their museums. A physiologist properly supported, and making a good use of his time, would do more for science by a residence of two years in the forests of the Orinoco than all the travels that have been undertaken since the time of A. von Humboldt.

Observations on the rise of temperature during flowering have hitherto been instituted on the *Araceæ* † alone. Lamark observed this fact in 1777 in *Arum Italicum.* Sennebier, Bory St. Vincent, and others ‡ subsequently communicated observations on the subject. The most exact and elaborate investigations are those of Vrolik and De Vriese. § According to them, the temperature has a regular periodicity within the twenty-four hours, and attains its maximum in the afternoon, between the hours of two and five. The difference between the temperature of the atmosphere and that of the root is sometimes as much as from 20—30° R. In this case, also, the probability is that the temperature is the result of a process of combustion. According to Th. de Saussure, the root of an *Arum maculatum* changed thirty times its volume of oxygen into carbonic acid in twenty-four hours. We are deficient, however, in comprehensive comparative observations, which should be made on crowded flower-stalks. The chemical processes ought to be measured with the greatest accuracy, and the temperature developed ought to be calculated and compared with the temperature observed. In all the cases which we have enumerated, the absolute temperature depends on the intensity of the vital process, and is higher in proportion to the vigour of the vegetation of the plants, or in proportion to the absorption of the sap and the vigour of its chemical processes.

Of these three phenomena, the first and last seem to have the same origin; the second is independent. Meyen maintains that the production of temperature in plants is peculiar, which may perhaps be due to the chemical processes that are constantly going on. But no result can be gained in the rude manner in which he pursues the subject. It is merely a guess to say that the temperature in the interior of trees must depend on the same causes as the development of temperature during germination and flowering. Thus much is certain, that, during the processes of germinating and flowering, carbonaceous matters are consumed and carbon is burned. In the process in the stem it is also certain that a formation of purely carbonaceous substances takes place, and it is as yet quite uncertain whether the chemical processes present absorb or liberate heat, because we are not yet acquainted with those processes. Meyen doubts the rising of the sap in winter, because roots are frequently found thoroughly frozen. But what roots? The difference of temperature between day and night disappears at a depth of 3′, and that between

* Poggendorff's Annalen, vol. xiv. p. 590.

† A complete enumeration of all these observations are to be found in the "Flora" (1842, vol. i. Supplement, No. 6, p. 84.).

‡ Meyen, Physiologie, vol. ii. p. 184.

§ Annales de Chimie et de Physique, vol. xxi. p. 279.

winter and summer at a temperature of 60—70′. Roots lying on the surface may be frozen, whilst those deeper may go on absorbing sap. An infinity of observations ought yet to be made in this field, and explanatory hypotheses are altogether inadmissible, as the facts to be explained are not yet known. Meyen, in this instance, falls into the same error of many other naturalists; they do not like to give up the flattering idea that science, with the exception of a few trifles, is quite complete, whilst in reality we have scarcely obtained an entrance into the wide field it ope n before us.

### B. *Development of Light.*

§ 212. Much has been written respecting the production of light from plants. If we separate, however, all fables and delusions from the real truth, but few facts will remain.

The whitish points of the black, and as yet problematical (?) fungus, *Rhizomorpha subterranea,* give out, according to A. von Humboldt, a peculiar phosphoric light. Meyen made similar observations on one of the *Algæ* (?), a species of *Oscillatoria.*

Decaying fungi, decaying wood, and other parts of plants, give out, it is well-known, light under certain circumstances.

The matter affording the light in these cases, consisting of a gelatinous matter, may be stripped off; and the light probably owes its origin to a slow process of combustion, at the expense of the atmospheric oxygen.

The daughter of Linnæus first observed a lightning-like phosphorescence in *Tropæolum majus* during a sultry, tempestuous night. This observation was subsequently confirmed in that and many other, generally yellow and orange-coloured flowers; every attempt at explanation respecting it is as yet impossible.

The following constitute the literature on this subject, which I have principally derived from Meyen's Physiol., vol. ii. p. 192, as I could not myself procure many of the works; and, indeed, I may add, that I could not see any utility in their study without an opportunity of instituting observations:—

Works on the general subject:—

Placidus Heinrich, über die Phosphorescenz der Körper.
Ehrenberg, vom Leuchten des Meeres.

On the especial subject of light in plants:—

Conrad Gesner, de lunariis. Zürich, 1555.

On *Rhizomorpha subterranea:*—

A. v. Humboldt, über unterirdische Gasarten. Braunschw. 1799.
Nova Acta A. L. C., vol. xi. pt. ii. p. 605.

On light in decomposing wood and other decomposing parts of plants:—

N. Act. A. L. C., vol. v. p. 482., and vol. xi. part ii. p. 702.
De Candolle, Flore franç. Paris, 1815, p. 45.
Link, Elementa Phil. Bot. ed. 1. p. 394.
L'Institut de 1836, p. 34.
Scherer's Journal der Chem., vol. iii. p. 12.

On light from the flowers: —

Kongl. Svenska Wetenscap-Academiens Handlingar, 1762, p. 284. (The observations of Linnæus's daughter on *Tropæolum*).

Bertholon de St. Lazare, de l'Electricité des Végétaux. Paris, 1783, p. 335. (*Tropæolum majus*).

Kongl. Wetenscap-Academien Nya Handl., 1778, p. 82. (*Helianthus annuus, Lilium bulbiferum, Tagetes spec.*).

Treviranus, Zeitschr. f. Physiol., vol. iii. pp. 257—269.

Hoppe, Botan. Taschenbuch f. d. Jahr 1809, p. 52. (*Tropæolum majus*).

Baumgärtner and Ettinghausen, Zeitschrift für Phys. und Mathem., vol. vi. pp. 459—462. (*Calendula officinalis, Tropæolum majus, minus, Lilium bulbiferum, Tagetes patula, erecta, Helianthus, Gorteria rigens*).

DeCandolle, Physiol. Végét., vol. vi. (?) p. 886.

DeSaussure, Chemische Untersuchungen über die Vegetation, translated into German by Voigt. Leipzig, 1805. (*Œnothera macrocarpa*).

Trommsdorff's Journal de Pharmacie, vol. viii. part ii. p. 52. (*Phytolacca decandra*).

Schweigger's neues Journal d. Chem. u. Phys., vol. i. p. 361. (*Polyanthes tuberosa*).

Sennebier, Physiol. Végét., vol. iii. p. 315. (*Arum maculatum* in pure oxygen gas).*

The giving out of light by the *Rhizomorphæ* and from decayed vegetables seems to be owing to the presence of a peculiar substance from which the light proceeds. Its nature, however, is by no means yet established, and we know nothing of its chemical properties. The existence of a chemical process, a kind of slow combustion, in this instance, is probable, first, from its analogy with the decomposition of vegetable substances in general, and also from the circumstance that this phenomenon does not always take place, but only under peculiar circumstances. Meyen says "it is no chemical process, but a phenomenon of expiring life, because it does not always occur." But the very reverse would follow from this. When, however, he asserts in page 205 "that it is the result of the *most intense* processes of life, or of *decaying* life, and probably is only an *intense* respiration," his probable meaning becomes, indeed, obscure and mystical enough.

In spite of the number of observations enumerated, it is yet possible that the giving out of light from flowers may be dependant upon an illusion, the same as occurs in the case of the *Schistostega osmundacea*, a small species of Moss, the proembryo of which Bridel-Brideri described as *Catoptridium smaragdinum*, whilst the great algologist Agardh proved that it was decidedly a new species of *Protococcus*. But it happens to be neither one nor the other, but the proembryo of the Moss mentioned, as Unger has proved beyond doubt.

The giving out of light from formless fluids, as from the milky juice of

* To this list I may add, that in the Transactions of the British Association for 1843, there is a notice of a "A luminous Appearance on the Common Marigold (*Calendula vulgaris*)," by Richard Dowden; and some remarks of my own on the same subject, in the Gardener's Chronicle for 1843. There are some interesting observations on "Phosphorescence" in Professor Matteucci's Lectures, before alluded to.—TRANS.

*Euphorbia phosphorea* (Martius, Reise nach Brasilien, vol. ii. pp. 726 and 746), belongs to physical and not botanical science.

### C. *Movements of the Parts of Plants.*

§ 213. Two kinds of motions of the parts of plants can be distinguished: 1st, those that are produced in the dead parts of plants by the change from the moist and dry state (§ 214.); and, 2dly, those which are caused in a manner as yet unknown to us, by changes in living cellular tissues (§ 215.).

A third kind of so-called movement, which does not belong here, brings a phenomenon of growth which determines the direction of certain parts, as the peculiar form of tendrils and the growth of the climbing plants.

Finally, those movements must be mentioned which entire plants are said to exhibit, as the *Oscillatoriæ* and some other forms of the lower *Algæ* (§ 215.).

The third form of phenomena alluded to above does not belong to true movements, although many consider them as such. It depends on the direction (the same takes place in the germinating plant when it is growing towards the light) given by an unequal tension of the cells on both sides, whereby that side is curved in which the cells grow least in the longitudinal direction. Similar irregularities occur, not unfrequently, in the extension of plants, but without producing any remarkable departure from their normal condition. They only create a tension, the effect of which only becomes visible when the continuity of the parts is interrupted by an accident. We may mention, as belonging to the same phenomena, the sudden curvature which particular parts of plants occasionally exhibit, as, for instance, the hollow flower-stalk of *Leontodon Taraxacum*, when it is split, or when a longitudinal strip is cut out of it, &c.

§ 214. The first kind of movements are either perfectly explainable, or, if not, it is owing to our inaccurate knowledge of the structural relations and other elements that demand attention, as the causes, remaining always the same, are known to us. All the phenomena under this head take place in the organs of plants, the elementary parts of which are either already dead or in the act of dying, but all of which are still of importance to the entire life of the plant; all, finally, are more or less connected with its reproduction by facilitating changes in the locality of the reproductive cells (spores or pollen-grains) or of the seed. We find phenomena of this description in almost all groups of plants. To such belong the valvular bursting of the species of *Geastrum* and some other *Fungi*, the opening of the spore-fruits, the movements of the teeth and the seta in Mosses, the bursting of the spore-fruits in the Liverworts, the tearing open of the same in Ferns, *Lycopodiaceæ*, and *Equisetaceæ*, the bursting of the anthers of the capsules, and the loosening of some parts of the fruit in *Euphorbiaceæ*, *Umbelliferæ*, and

*Geraniaceæ*, and the bursting of the hardened endocarp, as in the Almond in the *Phanerogamia*.

The causes are owing, 1stly, to the universal property of vegetable membrane to contract when in the act of drying up, and that the more so if their chemical nature is the same, the thinner the membrane; and if it is composed of different substances, the more so, the more they approximate in their quality to jelly; 2dly, the elasticity (however slight) of the vegetable membrane, which, when filled by fluids, is in a state of tension, and which again contracts when these fluids withdraw themselves; 3dly, to the contraction of a thin-walled cell filled with fluids, which, when the fluid escapes, is either not at all, or only imperfectly filled with air. These causes produce the movements enumerated, the different structure and nature of the cells in the same part of the plant causing an unequal contraction and, with it, a twisting or turning.

Although the phenomena here enumerated are generally known, I cannot find anywhere a more accurate analysis of the facts that they are based upon. Indeed, this could not be expected when such perfectly erroneous views of the nature of the vegetable membrane are adopted, as those of Link and Meyen.

The fact is well known, that vegetable membrane (and, in consequence, also the elongated cells, called vegetable fibres) extends when in a moist state, and contracts when in a dry state. Link has asserted the reverse of this (Elem. Phil. Bot., vol. i. p. 360), and Meyen (Physiologie, vol. i. p. 30.) has invented for it a singular theoretical explanation. I have contradicted this erroneous assertion (Wiegmann's Archiv, 1839, vol. i. p. 274.). Skulls are separated in anatomical researches by filling them with dry pease and putting water into them; rocks are burst by wooden wedges that are moistened; if we let fall a drop of water upon paper, it will form a vesicular elevation; the same takes place on thin boards: and numerous other similar well-known facts might be enumerated. Vegetable substances have frequently been used for hygrometers; for instance, Dalancé's strips of paper, Hautefeuille's, Täuber's, Ferguson's, Coniers', Anderson's, and Franklin's strips of wood, which exhibit, by the amount of their extension, the amount of humidity of the atmosphere. John Leslie constructed a hygrometer of boxwood, similar to Deluc's ivory hygrometer, the former being distended, when wetted, twice as much as ivory (Gehler's Wörterbuch, art. Hygrometrie). Others have used other vegetable substances, for instance, strips of fuci, for hygrometers. In answer to my observations, Link says (Wiegmann's Archiv, 1841, vol. ii. p. 407.), "Through disputes that were once carried on between DeLuc and Saussure respecting the hygrometer, it has been proved that dry vegetable fibre contracts by moisture, whilst animal fibre is elongated by it." This statement is altogether *untrue*, because the question of any material difference between the animal and vegetable fibre was never raised in the discussions of DeLuc and Saussure. But even had this assertion been made by one of them, it could from well-known facts be proved to be a decided error. Link seems to know nothing of the matter but by hearsay, for the result, especially of DeLuc's investigations, was clearly that no difference takes place in this respect between the animal and vegetable parts, excepting a quantitative one. DeLuc, in his Treatise

on Hygrometry (Philosoph. Transactions, vol. lxxxi. Parts I. and II.), distinguishes very minutely the *double* effect which humidity exercises on hygroscopical substances, both of animal as of vegetable origin: viz., 1stly, the distension of the membrane or fibre itself, which invariably takes place in *both* by the absorption of moisture; and, 2dly, the contraction which takes place in both of entire portions (especially of spiral ones) by water getting between the separate fibres (or between the cell-walls), which are thereby bent, and thus far produce a contraction of the individual part, notwithstanding the simultaneous distension of the membrane. The phenomena of hygrometrical substances are connected with both causes, and the sum total of the result must be exhibited according to the predominance of one or the other of these causes, either as a distension or a contraction. How the relations vary in this respect will be shown by the following table from DeLuc, which proves, at the same time, that all vegetable, as well as animal substances, can be distended by moisture. The second effect, however, begins to manifest itself at 100°, and a gradual contraction then takes place also in animal substances.

*Table of the relative Rates of Humidity in different Fibres of Vegetable and Animal Substances, taken longitudinally.*

| | Thorny Hair of a Porcupine. | Whalebone. | Hair. | Cat-gut. | Pita Flax. | Goose Feather. | Firwood. | Grass. | Longitudinal Strips of Box-wood. | Transversal Strips of Box-wood. |
|---|---|---|---|---|---|---|---|---|---|---|
| Highest degree of dryness. | 0·0 | 0·0 | 0·0 | 0·0 | 0·0 | 0·0 | 0·0 | 0·0 | 72·8 | 0·0 |
| | 18·0 | 12·0 | 15·6 | 9·7 | 20·6 | 37·0 | 33·2 | 26·8 | 87·4 | 4·5 |
| | 34·0 | 29·9 | 29·4 | 19·2 | 35·1 | 66·6 | 54·8 | 48·4 | 93·2 | 9·5 |
| | 48·8 | 39·9 | 40·9 | 26·8 | 51·6 | 78·7 | 74·9 | 67·1 | 97·8 | 14·5 |
| | 62·3 | 50·8 | 50·5 | 37·0 | 57·6 | 88·0 | 84·6 | 76·1 | 100·0 | 20·0 |
| | 73·3 | 58·8 | 59·2 | 47·1 | 75·6 | 93·4 | 89·8 | 83·9 | 95·9 | 25·7 |
| | 81·0 | 65·3 | 68·8 | 57·3 | 71·9 | 97·2 | 93·8 | 90·5 | 92·7 | 31·5 |
| | 86·8 | 70·8 | 73·0 | 67·4 | 76·3 | 99·0 | 96·0 | 95·1 | 88·6 | 38·0 |
| | 90·8 | 76·1 | 78·3 | 75·6 | 83·0 | 94·4 | 94·3 | 98·6 | 79·9 | 45·5 |
| | 93·0 | 81·4 | 82·1 | 82·9 | 86·6 | 96·2 | 97·7 | 100·0 | 70·3 | 51·5 |
| | 95·0 | 85·4 | 86·1 | 87·8 | 93·6 | 99·0 | 100·0 | 98·8 | 63·9 | 56·5 |
| | 94·5 | 88·4 | 88·8 | 91·6 | 96·5 | 95·3 | 94·6 | 98·0 | 57·3 | 61·2 |
| | 97·0 | 90·8 | 91·6 | 94·7 | 94·7 | 97·2 | 97·0 | 97·2 | 51·0 | 65·7 |
| | 96·5 | 92·8 | 93·8 | 96·3 | 98·2 | 98·2 | 94·6 | 96·2 | 45·7 | 69 7 |
| | 96·5 | 95·2 | 95·6 | 97·8 | 100·0 | 100·0 | 93·0 | 94·8 | 40·9 | 73·7 |
| | 95·0 | 97·1 | 97·2 | 98·7 | 99·2 | 99·0 | 91·4 | 92·6 | 31·4 | 77·7 |
| | 97·0 | 98·1 | 98·0 | 100·0 | 98·2 | 98·2 | 89·0 | 89·8 | 21·7 | 81·5 |
| | 98·0 | 99·1 | 100·0 | 98·7 | 96·8 | 97·2 | 86·9 | 86·5 | 16·0 | 85·9 |
| | 98·6 | 99·6 | 100·0 | 96·8 | 94·1 | 95·3 | 84·6 | 84·0 | 10·4 | 90·5 |
| | 99·1 | 100·0 | 99·3 | 94·5 | 91·5 | 94·4 | 81·9 | 80·9 | 5·1 | 95·5 |
| in the Water. | 100·0 | 99·5 | 98·3 | 91·8 | 88·3 | 92·5 | 77·0 | 77·0 | 0·0 | 100·0 |

Next to the boxwood (cut longitudinally) a twisted hemp rope ought to be enumerated, in which, in consequence of the close junction of the fibres, the second effect takes place still earlier. This is the result of scientific research upon this subject; and Link's assertions to the contrary are the result of sheer ignorance.

It is a very common thing to hear general phrases made use of respecting hygroscopicity as the result of desiccation, &c., without any

reason being assigned as to how this effect is brought about. It appears to me that the three following points ought to be distinguished :

1. Vegetable membrane is certainly only elastic in a slight degree ; it may be distended as almost all other organic substances, but again resumes its former volume on the withdrawal of the tension. The parenchyma of the living plant, in consequence of endomosis, is constantly in a state of tension ; each cell occupying a greater space than belongs to it according to the natural circumference of its membrane. On removing, however, a portion of the liquid thus distending it, the cell contracts to its natural size. This effect, trifling as it may be in the single cell, must yet become perceptible when hundreds of cells are taken into consideration. Microscopical observation proves that this is really the case. If we cut off the larger part of a succulent plant when it is distended with fluid, as the joint of an *Opuntia*, or a large succulent leaf, and allow it to remain for a short time in a dry place, the loss of weight will prove to us that a part of the water has evaporated, and exact measurements will prove that a simultaneous, but very slight, contraction to a smaller volume has taken place. Nevertheless, however, we find all the cells entirely filled with juice, even on the most accurate microscopical examination: and none exhibits in its membrane the slightest fold, all appearing in a state of absolute tension. Simultaneously, therefore, with the evaporation of the water, there must have taken place a slight contraction of all the cells. Let us apply this to the external succulent layer of parenchyma in the fruit of the almond. When distended by juice, the number of cells suffices perfectly to enclose the hard stone, which is but little changed in volume by the process of drying. But when the cells, becoming ripe, gradually lose their fluid contents (which are no longer supplied by the fruit-stalk), a stretching takes place by means of the contraction of the individual walls of cells that are firmly connected with each other, the envelope becomes too narrow for the stone, and if, as really occurs, there happens to be a layer of cell tissue in which the cohesion is not so strong as the expanding power, this layer is torn, and the cleft thus caused becomes wider the further the evaporation of the water proceeds.

2. To this condition we must add, as its continuation, a second and a much more remarkable phenomenon. The thin membrane of the cell is flexible in the highest degree, and on the liquid evaporating from the cells without their being simultaneously filled with air, the cell diminishes in volume from the pressure of the external air, in the same way that an animal bladder filled with water, gradually losing its water without the vacant space being filled with air, cannot be distended to its former volume without being torn.

3. Vegetable membrane is very hygroscopical, and becomes distended by moisture and contracted by dryness. But both take place in a very different degree, according to two concurring circumstances. The more the membrane approaches, in its chemical constitution, jelly, the more it contracts when in the act of drying up; and the more it approximates to the nature of perfectly developed cellulose (membranenstoff), the slighter is the expansion when exposed to the action of moisture. The membrane, when of the same chemical nature throughout, appears to contract the more the thinner it is, and the less the more it is thickened by secondary deposits. This latter view agrees with the circumstance that all spiral fibres (which, as we are in the habit of isolating them, consist externally of the spirally-torn primary cell-membrane, and internally

of the deposit-layers) become straight on drying, but again roll up on being wetted, because the primary cell-membrane contracts in a dry and expands in a moist condition.

I have hitherto been able to make, respecting these facts, only a few experiments, which, although they do not afford anything like correct figures,—for I will admit a probable error of ten per cent.,—yet, relatively speaking, they have their value. The following are the results:—

*Polyides lumbricalis*, moderately thick-walled, gelatinous cells, and the rather swollen extremity shortly before the formation of spores=*A*. *Laminaria digitata*, a piece of the flat *frons*=*B*. *Sphærococcus crispus*, somewhat thicker cells of the *frons*=*C*. *Sphærococcus cartilagineus*, rather thick cells, a piece of the round peduncle of the *frons*=*D*.; measured in a dry state (all the measures are given in millimetres)=*a*, after having been lying in the water for 3 hours=*b*, after 24 hours' soaking in water=*c*, amount of the prolongation in decimals of the original length=*d*.

| | *a*. | | *b*. | | *c*. | | *d*. |
|---|---|---|---|---|---|---|---|
| | Length. | Width. | Length. | Width. | Length. | Width. | Length. |
| *A*. | 26·5 | 1·5 | 37·5 | 2 | 39 | 2 | 0·471 |
| *B*. | 63 | 11 | 71·5 | 16 | 72 | 15 (?) | 0·142 |
| *C*. | 16·5 | 3 | 19 | 5 | 19 | 5·5 | 0·181 |
| *D*. | 17 | 1·5 | 18 | 2 | 18 | 2 | 0·052 |

*E*. Fibres of hemp (very elongated cells, thick-walled, the light disappearing under the microscope, cellulose well developed) were suspended in a glass tube, which was wider below, and enclosed in it for 24 hours with chloride of calcium, and then measured=*a′*. The chloride was removed; the end of the tube, which was open below, was immersed in water, and measured after 24 hours=*b′*. The tube was then filled with water, and again measured after the fibres had been 24 hours in water=*c′*. During this process the temperature of the room fluctuated between 10° and 18° R. Finally, the tube was emptied of its water, and dried, with the fibres, over chloride of calcium at about 30° R., and again measured=*d′*. The amount of the greatest elongation in decimals of the original length gives *e′*. The fibres 1 and 2 had at their end the weight of a small shot, which was scarcely heavy enough to stretch them straight; the fibre 3 had upon it a rather heavier shot.

| | | *a′*. | *b′* | *c′* | *d′* | *e′* |
|---|---|---|---|---|---|---|
| *E*. | 1. | 469 | 470 | 470 | 468·5 | 0·0021 |
| | 2. | 434 | 434·5 | 434·5 | 434 | 0·0011 |
| | 3. | 951 | | 594·1 | | 0·0036. |

*F*. In the month of February a shoot of *Salix alba* of the previous year was cut off and placed in water for 24 hours, at a temperature of 10° to 15° R.; the bark was then taken off, and the length measured=*a″*; it consisted entirely of alburnum, therefore of slightly thickened and elongated cells with imperfectly developed cellulose: the small pith may be here overlooked. The twig was now dried at a temperature of 10° to 15° R., and the length again measured=*b″*; finally dried for

24 hours at 30° R., and the determinate length=$c''$. The amount of the greatest prolongation in the humid state was then calculated in decimals of the original length=$d''$.

| | $a''$ | $b''$ | $c''$ | $d''$ |
|---|---|---|---|---|
| *F.* | 260 | 259 | 258·5 | 0·0058. |

*G.* A strip was cut from the axis of a fresh, straight, thick shoot of a *Stapelia*, and its length determined=$a'''$, its width and thickness=$b'''$. It consisted entirely of thin-walled parenchyma cells, consisting of perfectly developed cellulose. It was fastened to a cork, and thus suspended in a glass flask, the bottom of which was covered with chloride of calcium. The length it became, after 24 hours' exposure with a temperature fluctuating between 10° and 15° R.=$c'''$, width and thickness =$d'''$, and the amount of the expansion in the humid state, calculated in the decimal fraction of the original length=$e'''$.

| | $a'''$ | $b'''$ | $c'''$ | $d'''$ | $e'''$ |
|---|---|---|---|---|---|
| *G.* | 189 | 8 | 174 | 3·5 | 0·086. |

The slight contraction that takes place at first in the thin-walled parenchyma cells, which consist of perfectly developed cellulose, is produced by means of elasticity, to which must be added the insignificant hygroscopical contraction of the membrane, whilst the action only becomes so striking through the falling together of the cells in consequence of the desiccation.

As an instance of the application of these phenomena to the explanation of the bursting of capsules, I may cite *Iris atomaria.* The upper half of the wall of the capsule, which separates itself from the other parts, and retracts, consists of the following layers. At the most external part there is an epidermis of flat, very irregular cells, the walls of which are rather gelatinous and slightly porous; then follow, towards the interior, several layers of parenchyma cells, which are at first flat, and become gradually somewhat rounder, and the walls of which are also rather gelatinous. The walls of the epidermal cells are moderately thick, the layer of parenchyma lying beneath are joined to the latter, the walls become gradually thinner, and, as it appears, are gradually converted into cellulose. Very thin-walled cells, which extend almost from the interior to the exterior, form an internal layer containing many intercellular spaces, into which layer the vascular bundles run. Then follows, almost suddenly separating itself from the former, a very thin layer of cells, which being rather thick-walled, and formed of firm cellulose, are about ten times as long as broad, and which laterally, for long intervals, frequently only touch each other, like stellate cells, by means of small processes, and which, arranged in different directions, are yet, on the whole, arranged in such a manner that their longitudinal diameter is horizontal. Finally, quite towards the interior, comes the epithelium, consisting of tolerably thick-walled, porous, elongated cells, the longitudinal diameter of which almost invariably forms, with the previous cells, an angle of 25° to 30°. The entire wall of the capsule, in a fresh state, is $1\frac{1}{2}$ to 2 millim. thick. The most internal of these layers, together with the epithelium, can contract only a very little, perhaps enough to enable it to tear the margins of the valves from each other. The external layers, on the other hand, must contract very considerably, both in length and width, as it is owing to this that the valves

are first of all torn on the external surface, then separate themselves from the point towards the basis as far as about the middle, curving themselves outwards. A complete separation of the valves, and a perfect tearing back, would, in consequence of the structure, here no doubt take place, if, firstly, the cells of the suture were not thicker below *, and capable of resisting the tension ; and, secondly, if the very thick and tough partition-wall was not placed upon the centre of the valves, which, like a prop, resists their curvature, and which last action is still further aided by the two longitudinal ribs, which project upon the external side of each valve.

The different movements of this kind are almost invariably produced by the co-operation of the three phenomena here explained. It cannot be expected that I should explain all possible cases, for which purpose the necessarily accurate anatomical facts are still wanting. Every one will easily be able to apply the above conditions to individual cases ; as an instance, let us take the tearing of the capsule in *Aspidium filix mas.* The capsule is flat, almost lenticular. A row of cells, commencing on the one side from the stipes, forms round the greatest part of the circumference an imperfect ring, leaving on the other side a vacant space, about one-sixth of the circumference. The cells are almost parallelopipedical, and their walls towards the cavity of the capsule, where they mutually touch each other (not towards the sides and exterior), are very much thickened. The lateral walls, which pass into each other at the before-mentioned one-sixth of the circumference, consist of very flat and extremely thin-walled cells. The thicker and tougher walls of the cells of the ring are but slightly, or not at all, changed by the process of drying, but the thinner walls of the same cells are so. On the evaporation of the fluid in the cells, they first contract in a somewhat elastic manner, and thereby shorten the distance between the extreme end of the thick walls, and thus of the whole external circumference of the ring ; but as the moisture continues to evaporate without being supplied with an equal quantity by air, the thin walls are pressed in by the atmospheric pressure, and the contraction of the external circumference of the ring is thus still more considerably increased. The internal circumference, consisting of cells with thickened walls, remains unchanged, but, through the contracted sidewalls that act as a rectangular lever, it receives a tendency to straighten itself. This tension only continues as long as the thin-walled cells at the last one-sixth of the circumference are capable of resisting the expanding power ; as soon as the tension becomes more powerful, they burst into a transverse slit, and the capsule is opened. The progress of this process is quite similar in the teeth of the capsules of the Mosses.

§ 215. The second kind of movements are seen in living parts of plants during vigorous vegetation, and depend probably on the distribution of the sap, and upon the elastic expansion of the individual cell-membranes. The facts, however, connected with this subject are as yet too little known to admit of a clear explanation. The following varieties of movements may be distinguished : —

* According to this, we can beforehand, by means of anatomical examination of the cells, determine, in valves that are not completely separated, how far separation of the valves will take place.

*A.* Movements which evidently depend on external influences, as

*a.* Periodical.

In many plants it is observed that the foliar organs, the leaves of the stalk as well as of the flower, assume a different direction during night from what they do in the day, and these phenomena are frequently produced by the brightness or the cloudiness of the sky. This, since the time of Linnæus, has been called the sleep of plants. In general, it may perhaps be assumed as a rule that the parts of plants during the absence of light resume as nearly as possible the position which they occupied in the bud, and this the more accurately the younger and more tender the leaf. The deviations arising in this respect from day and night are slighter in older and tougher leaves; they disappear entirely in perennial and leathery leaves. The very compounded leaves of the *Leguminosæ* and *Oxalidaceæ* exhibit these phenomena in the most striking manner.

Similar movements may be observed in some flower stalks, which are curved during night in such a manner that the flower is turned towards the ground; for instance, *Euphorbia sp.*, *Ranunculus polyanthemos*, *Draba verna*, *Verbascum blattaria.*

In opposition to this, there are some few flower leaves which deviate from their normal position in the bud during night, and again return to it in the day; for instance, *Mesembryanthemum noctiflorum.*

The movements here mentioned, especially of the first kind, are so remarkable in some plants that even Pliny observed them (N. H. viii. 35.) But Linnæus first of all traced them more accurately, and published an elaborate account of them. (Somnus plantarum. Upsaliæ, 1755, Amœnit. Acad. vol. iv. p. 133.) The number of observations has subsequently increased, and every one may by individual researches confirm the matter. I am of opinion that it is based upon the same cause as the phenomena which will be spoken of under *b.* The anatomy of the parts in which the movement takes place should be examined in a larger series of plants, and the state of the cellular tissue, especially in the day, should be accurately compared with the state which it exhibits at night; exact measurements should also be made of it. The movements are observed most frequently and most strikingly in that region where the petiole of the leaf passes into the stalk, and where the petiolules pass into the common petiole of the leaf, particularly when that swelling of the cellular tissue called the *pulvinus* is very considerable. But experiments in which the *pulvinus* has been carefully stripped off seem to prove that the cause of this motion is not seated in this part, as Dutrochet supposed.

With regard to the facts of the present paragraph, I have no observations of my own to offer, and therefore merely communicate the most essential of these facts. I must refer to Meyen's Physiologie (vol. iii. pp. 473—562.) and to Dassen's works (the principal work quoted by Meyen*) for details, and more especially respecting the results of ex-

* Natuurkundige Verhandelingen van de Hollandsche Maatschappij der Wetenschappen te Harlem II. Deel. Te Harlem 1835, pp. 309—346. and: Tijdschrift voor natuurlijke Geschiedenis en Phys. 1837, vol. iv. pp. 106—131.

periments which were instituted, and which, according to my view, were very imperfect. The conclusions which Meyen comes to from experiments of his own and of others, are for the most part unfounded, and are most intimately connected with his prejudice of an analogy between plants and animals. He evidently very frequently obtains the results which he previously wished to arrive at.

*b.* Not periodical.

Perfectly similar movements to those which occur gradually on the change of day and night are exhibited by the leaves of some plants suddenly, or at least with great rapidity, as soon as they are brought under the influence of any external chemical or mechanical agency. The following are pretty nearly all the plants in which these phenomena have been observed: —

*Mimosa pudica* L., *M. sensitiva* L., *M. casta* L., *M. viva* L., *M. asperata* L., *M. quadrivalvis* L., *M. pernambucana* L., *M. pigra* L., *M. humilis* Humb., *M. pellita* Humb., *M. dormiens* Humb.

*Æschynomene sensitiva* L., *A. indica* L., *A. pumila* L.

*Smithia sensitiva* Ait.

*Desmanthus stolonifer* DeC., *D. triqueter* DeC., *D. lacustris* DeC.

*Oxalis sensitiva* L.

*Averrhoa Carambola* L., *A. Bilimbi* L.

The movement of the leaf of *Dionæa muscipula* Ell., supported by a winged petiole, appears peculiar. The leaf is furnished with cilia, and on the upper surface covered with stiff hairs. On this surface being touched, for instance, by an insect, the leaf closes together along the central nerves, and the cilia fold within one another, so that the object brought in contact with it is enclosed, and held fast with some force as long as the movement continues. On the latter ceasing, the leaf slowly expands again. In this manner irritable insects are kept captive till they are dead.

The reproductive organs in some of the *Phanerogamia* exhibit a sudden movement in consequence of external influences which produces a transference of the pollen from the anther to the stigma. By way of example, we may mention the stamens of *Berberis vulgaris*, *Parietaria judaica*, the style of *Stylidium adnatum*, *S. graminifolium*, *Goldfussia anisophylla*, &c. The movement takes place also in this case without an external cause, although not so rapidly.

It cannot be denied that the so-called Sensitive plant (*Mimosa pudica*), which folds up its leaves from the shaking of the ground caused by the tramp of a horse, and at every rude touch, presents a most welcome object for poetic treatment; and the circumstance of this plant not having been known to the old Greeks has certainly made us poorer by one beautiful myth at least. The task of the naturalist, however, is different; he has other problems to solve, and to him this plant, and its relations in time, must for the present be a land-mark indicating to him the boundary of his knowledge, and a significant warning not to people with the mere creations of his fancy that domain which demands of him earnest and true work. A glance at all that has been done with

respect to this plant proves to us very clearly that, with regard to the palpable parts of the phenomena, we have only obtained a mere sensationary knowledge of the rudest external aspect of the mechanism of these motions, and that elaborate, careful researches must precede our arriving at the point when the question of the cause of this phenomenon can be put, and an explanatory theory of the movement can be proposed. Until that time arrives, the reflective naturalist had better not enter into any examination of hypotheses, or criticisms upon the explanations of others. The uselessness of such a proceeding is evident. It would be time wasted, — time which might be much better devoted to the investigation itself.

Meyen, as has already been observed, has taken immense pains to arrive at a conclusion, and in which, by means of some break-neck leaps by way of inferences, he actually seems to have succeeded. Some experiments, however (the only ones which I once had an opportunity of instituting with a *Mimosa pudica*), proved to me how little has as yet been truly ascertained on this point, since they furnished me with results almost directly contrary to the statements of Meyen. The matter stands thus: Meyen experimentalised on some very susceptible plants, kept at a high temperature, being of opinion that this is the only way of arriving at correct results. But this is opposed to correct practice, as the least susceptible and strongest organisms are always selected for experiments, by way of preference, in order to avoid unintentional secondary interferences with the result of the experiment. A *Mimosa*, which is so susceptible that it closes *all* its leaves upon the least shaking of the ground, is certainly not well calculated for the purpose of showing that it only closes some particular leaves on the division of its vascular bundles. I purposely caused my plant, therefore, to vegetate for some time at a low temperature, so that it did not close its leaves on slight shakings; and the result was, that I found almost every thing different from what Meyen had stated. It appeared to me that the loss of sap beneath a leaf was invariably followed by a depression of the leaf, which continued until the wound was closed by the coagulation of the sap. It is not, however, worth while to communicate the details of these isolated observations, since, so long as we are ignorant of the mechanism of the motion itself, they could only give rise to useless guessing respecting the cause. I can only assert again, that, hitherto, we are not only unacquainted with the cause, but perfectly unacquainted even with the specialities of the fact itself; and the same may be said of the movements of the other plants mentioned.

*B.* Movements independent of external influences.

*a.* Periodical.

These are seen in some tropical species of *Hedysarum*, especially *H. gyrans* L. and *H. gyroides* Roxb. The movements of the first plant are known best of all, and are double. The compound leaf in these plants consists of a couple of small lateral leaflets, and of a large terminal leaf. The latter and the common petiole move up and down according to the varying intensity of the light; and the terminal leaf is, especially in its changes of position, a most delicate photometer. These movements evidently correspond with those enumerated under *A.*, *a.* The two lateral leaflets, however, exhibit a constant vibrating movement, every leaflet describing a

little circle with its point, but in such a manner that the axes of both leaflets always remain in a straight line. This motion is entirely independent of light, of day and night, and is increased by heat and by a more luxuriant vegetation of the whole plant. No explanation can be given of this phenomenon.

*b.* Not periodical.

Such movements take place in most of the *Phanerogamia*, with the object of transferring the pollen upon the stigma; the stamens and stigma approaching either one or the other, or both changing their position. In many plants, the stamens assume again a different position after they have distributed the pollen. These movements can no more be explained than the others.

§ 216. The phenomena exhibited by the *Oscillatoriæ*, a small genus of *Algæ*, are very remarkable; the species appear to consist of short fibres composed of cylindrical cells united to each other, which are broader than they are long, and filled with a green matter and other contents, which are partly liquid and partly granular. The point of every fibre is somewhat contracted and rounded, frequently as clear and colourless as water. As long as they vegetate vigorously, these fibres exhibit a three-fold movement an alternating slight curvature of the anterior extremity, a half pendulum-like, half-elastic bending to and fro of the anterior half, and a gradual advancing movement. These movements are frequently observed to occur simultaneously, and often, also, separately. The causes are perfectly unknown.

The movements of the *Oscillatoriæ* have something strange, I feel almost inclined to say something mysterious, about them. I will not conceal my opinion, which is entirely based upon a subjective feeling, that their position in the vegetable kingdom appears still doubtful to me. At all events, it appears to me to indicate a very hasty judgment for any one, as Meyen has done, to ridicule those who hold such an opinion. Our knowledge of these organisms is very defective, and although Ehrenberg refers them to plants, this is by no means a proof of their vegetable nature, but rather of Ehrenberg's modest caution,—a quality of which it would be very desirable that Meyen should possess a little more, and which would prevent him going further than exact and certain observations would warrant. Meyen further associates this movement with those of *Spirogyra*, which contracts spirally, and remains so. I have never observed it: I do not deny it. But when he states that the plant creeps upwards on the walls of vessels in which it is kept, and that this is not the case with any other *Algæ*, he states that which is false, and which can be easily disproved, for the *Algæ* grow naturally up the sides of a glass vessel, and the water they need follows them through the action of capillarity.

All other so-called *Algæ* of the families of *Bacillariæ*, *Desmidieæ*, &c. are, according to Ehrenberg's observations, of yet too doubtful a nature to afford them a space in this work.

* Recent investigations on these families in Great Britain have induced some botanists to adopt them unreservedly into the vegetable kingdom. See Lindley, Vegetable Kingdom, p. 12. 1846. Ralfs, The British Desmidieæ. 1848.—Trans.

# CHAPTER II.

## SPECIAL ORGANOLOGY.

§ 217. THE object of Special Organology is to develope the functions of the individual organs of plants, and we have now principally to give here a synopsis of what has already been presented in other parts of the work. The result of the whole will be that, excepting the organs of reproduction, the plant possesses *no definite physiological organs at all*, namely, such as perform one certain, determinate function. Our knowledge respecting these functions is as yet very defective, and with regard to the *Angiosporæ* we are almost entirely without observations.

The best method of distributing the matter will be to regard the organs of reproduction independent of the other organs (those of vegetation), and to divide the former into *Cryptogamia* and *Phanerogamia*, including the *Rhizocarpeæ*; and the latter into *Angiosporæ* and *Gymnosporæ*.

### A. *Organs of Vegetation.*

#### a. *Angiosporæ.*

§ 218. As organs are almost out of the question in the whole group of the *Angiosporæ*, we have only to consider here the tissues and elementary parts. The organs for attaching or fixing the plant to the ground can only be mentioned as having a certain locality, but most of them also grow with the plant when detached from the ground. The whole external surface is only intended to receive nutritive fluids; and this is all we know of these plants. With regard to the Lichens, the green, round cells may occasionally project from beneath the bark, and become new plants when dispersed about; this is probably the case in the other orders, but has not yet been observed.

#### b. *Gymnosporæ.*

§ 219. The leaf and axis, as fundamental organs, have no determinate physiological functions, except such as belong to them in their metamorphosis into reproductive organs. As, however, the axis originally forms the connecting link of all parts, and alone is of a permanent nature, whilst the leaf, on the other hand, is subsequently formed and dependant, is isolated and transient, so we may say that the function of the distribution of the sap belongs

principally to the former, for through it all the currents must pass; whilst, on the other hand, the processes of secretion principally take place through the leaf.

§ 220. No essentially different functions can be attributed to the different forms which the axis exhibits. With regard to the distinction of the two poles, the root and the axis, in a limited sense, the former is frequently an organ of attachment, which fixes the plant in a certain spot, and, from its being in contact with fluid matters, serves especially for the absorption of nutriment; it is likewise a secreting organ, and, through the formation of buds, serves the reproduction of the plant.

That none of these functions are essentially and exclusively connected with the roots, is proved by their never being found in Mosses and Liverworts; and also by their undeveloped state in so many other plants, for instance, many Grasses, *Nelumbium*, &c.; and finally, their decay in other plants, for instance, in Ferns, Palms, *Cuscuta*, &c. Their absence in all these plants is not supplied by secondary roots, which might wholly or in part perform these functions; for instance, *Ceratophyllum* remains perfectly rootless in every sense of the word.

The functions of the axis, in a limited sense, can only be divided according to anatomical systems, and not according to its various morphological organs. The vascular bundles, where they exist, serve in their youngest parts (the cambium) for the distribution of the sap; in their older parts they serve as a stiff and firm hold (skeleton) for the plant. The parenchyma assimilates, and forms all the peculiar substances which occur in the plant. Its external parts (back and epidermis) serve for the absorption of nutritive fluid, and also for secretion in plants under water, and for respiration and transpiration in plants exposed to the air. In their subsequent state, after the cellular layers of the bark have been formed, the bark serves, on account of its being a bad conductor of heat, as a means of maintaining the temperature of the interior of the plant. Finally, the axis is an important organ of reproduction, on account of its frequent regular and irregular development of buds. In peculiar forms, as in cirrhi or in climbing plants, the axis becomes an organ of attachment.

§ 221. The leaves are mostly very independent of each other, and exhibit great variety in their chemical processes, according as they are stem-leaves or flower-leaves. The stem-leaves, being those parts of the plant which expose the largest surface to the air, form principally the organs of respiration and transpiration, as also of various secretions. In plants growing under water, they serve for the absorption of fluid nutritive matter. By the formation of buds they become organs of reproduction. The leaves in the region of the organs of fructification frequently exhibit a very weak vegetation, and easily die altogether (for instance, the pappus, the bracts, and

bracteoles of the *Paronychiaceæ*), or if not, at least partially (as in many white flowers), or are so far dead that their cells are entirely filled by special matters or substances not calculated to sustain chemical processes (as most of the coloured bracts and petals). It is only the calycine and carpellary leaves that exhibit an active vegetation not different from that of the stem-leaves.

The function of protecting the tender, newly-developed parts by a firm enclosure around the buds against the influences of the atmosphere, and against excessive moisture which readily produces decomposition, belongs to all leaves, without any exception. They continue to protect these tender parts until the development of the epidermal system enables them to resist these injuries. This last-named function seems to be that which is more especially performed by calyx and corolla. As soon as the flower has opened itself, the sepals and petals may be removed without injuring the development of the seed and fruit in the slightest degree, provided they do not still serve the purpose of protecting the tender organs of reproduction against rain, &c.; or if, after their removal, the transfer of the pollen to the stigma is rendered impossible, an artificial transfer is substituted.

The leaves also become organs of attachment in the form of cirrhi.

## B. *Organs of Reproduction.*

### a. *Cryptogamia.*

§ 222. Among the *Angiosporæ*, the sporangia are the only parts to which we can attribute a definite function, namely, that of forming the spores, of which they are the parent-cells. We know nothing of the object of the other parts of the sporocarp, and, indeed, it is very improbable that they should possess any other than a morphological significance. The nature of the so-called anthers has been already explained (§ 84.).

There are likewise parent-cells of the spores in the *Cryptogamia* and *Gymnosporæ*, which, as such, exercise an important function. The sporocarps only serve as envelopes of the spores, and facilitate and regulate the distribution of the spores by their hygroscopic properties. With regard to the *Antheridia*, we can state for certain, that not a single fact exists from which we could infer, in the remotest degree, that they have the slightest connexion with the function of reproduction. Every thing that has been hitherto written on this subject are only fine-spun fancies, founded upon decidedly false analogies.

It may be further stated, that we are still ignorant with regard to the peculiar function possessed by the external spore-case in relation to the development of the spore. It is possible that it may be principally intended, through its indestructibility, for the protection of the delicate cell of the spore against injurious agencies

and the action of humidity, until the cell itself is in a state fit to assimilate foreign matters.

### b. *Phanerogamia.*

§ 223. With regard to the anthers, the parent-cells form the pollen, and the external, and frequently so richly and curiously-formed membrane seems to perform no other function than that of the spore-case alluded to at the conclusion of our last paragraph. The formations, secreting surfaces, or organs that secrete sweet juice, the true nectar, have no imaginable organic connexion with the function of reproduction; but they appear to attract the insects, which latter so frequently assist in the transfer of the pollen to the stigma.

The seed-bud (ovule) is intended for the reception of the pollen-tube. It is protected by the germen in the same manner as the terminal shoot is by the external leaves of the bud, and at the same time it conveys to it the pollen-tube.

The most important part of the seed-bud is the embryo-sac, because the embryo (with the exception of the *Rhizocarpeæ*) is developed in it. We are as yet entirely ignorant of the influence which this sac exercises on the embryo.

It is certain that granules of pollen produce *genuine* tubes in other spots besides the stigma; it is also certain that many pollen-tubes descend through the stigma and style into the cavity of the germen, *without* being converted into embryos, because they have not penetrated the seed-bud. But it is likewise as certain, that the tubes in the *Rhizocarpeæ* do not come into immediate contact with the embryo-sacs, being constantly separated from them by a thin layer of cells. An observation of my own, referred to on a former occasion *, is also highly remarkable, viz., that two pollen-tubes entered into the seed-bud of an Orchid, one of which, penetrating through its internal opening, reached the embryo-sac, and pressing upon this was converted in the usual way into an embryo, whilst the other penetrated between the external and internal covering of the seed-bud, and was developed into the rudiment of an embryo (a kind of *graviditas extrauterina*) (see Plate VI., fig. 1.). It appears, therefore, that the influence of the embryo-sac may extend to some distance, but it is entirely unknown to us what kind of influence; and it is the more difficult to be discovered, as the most important elements in the enquiry, viz., an accurate chemical investigation of the contents of the pollen-tube and of the embryo-sac, are not yet forthcoming, and are not likely to be so for a long time to come. I may here remind my readers of Caspar Fr. Wolff's expression, "*Nutrimentum magnum in minima mole.*" As to analogies between the production of plants and the procreation of the higher animals, it can merely afford employment for the wit of those who have nothing better to do, since the act itself, and the part which the different materials play in it, are as yet entirely unknown to us, even with regard to the higher animals.

* Acta. Acad. C. L. C. N. E. vol. xix. pt. i. p. 46, in *Orchis latifolia.*

§ 224. At subsequent periods the plant, which is gradually developed from the embryo, is decidedly nourished by the embryo-sac, and even afterwards, in the later stages of germination, the assimilated substances deposited in the endosperm serve for the sustenance of the plant. The nucleus of the bud performs a similar function with the perisperm, and acts as a substitute for the latter. The envelopes of the bud are converted into the testa of the seed, and protect the delicate germinating plant; the envelopes of the fruit perform the same function, and subsequently assist in the distribution of the seed by means of their hygroscopicity. The succulent parts of the fruit may also serve, through their decay, to form a nutritive soil for the first development of the young plant.

## *Conclusion.*

The insufficiency and deficiency of our generalisations in Botany are acknowledged by all competent investigators. It was believed that more favourable results might be expected as Physiology and Anatomy advanced, and systematic Botany looked for aid from the same sources. The meagreness of our Physiology, freed from all that does not properly belong to it, as I have endeavoured to give it, affords but little hope at present from that quarter. It cannot have escaped the notice of the attentive reader of the Morphology, that little also can be expected from Anatomy. Whence, therefore, are we to look for help? By the study of external forms; not in the manner that it has hitherto been done, superficially and without fundamental principles, but from the study of Morphology as a science, whose leading principle must be *the history of development.* It has been my object in the present work to indicate the proper path, and to open an entrance into it according to the best of my ability. May better men continue the work!

# APPENDIX.

## A.

### ANALYTICAL PAPERS BELONGING TO THE DIVISION RESPECTING THE NOURISHMENT OF PLANTS.

#### I. Boussingault's Experiments, communicated in his "Economie Rurale," Vol. II.

a. *Tables showing the Contents of Water in the Vegetable Matters analysed in Boussingault's Experiments.*

| | Dry Matter. (dried at 110° C.) | Water. |
|---|---|---|
| Wheat | 0·855 | 0·144 |
| Rye | 0·834 | 0·166 |
| Oats | 0·792 | 0·208 |
| Wheat Straw | 0·740 | 0·260 |
| Rye Straw | 0·813 | 0·187 |
| Oat Straw | 0·713 | 0·287 |
| Potatoes | 0·241 | 0·759 |
| Beetroot | 0·122 | 0·878 |
| Swedish Turnips | 0·075 | 0·925 |
| Topinambour | 0·208 | 0·792 |
| Pease | 0·914 | 0·086 |
| Pease Straw | 0·882 | 0·118 |
| Clover Hay | 0·790 | 0·210 |
| Stalks of Topinambour | 0·871 | 0·129 |

b. *Composition of the Manure* (dried in a vacuum at 110° C.).

| | Carbon. | Hydrogen. | Oxygen. | Nitrogen. | Salts and Earths. |
|---|---|---|---|---|---|
| I. | 32·4 | 3·8 | 25·8 | 1·7 | 36·3 |
| II. | 32·5 | 4·1 | 26·0 | 1·7 | 35·7 |
| III. | 38·7 | 4·5 | 28·7 | 1·7 | 26·4 |
| IV. | 36·4 | 4·0 | 19·1 | 2·4 | 38·1 |
| V. | 40·0 | 4·3 | 27·6 | 2·4 | 25·7 |
| VI. | 34·5 | 4·3 | 27·7 | 2·0 | 31·5 |
| Average | 35·8 | 4·2 | 25·8 | 2·0 | 32·2 |

The Analysis shows that the quantity of manure, which is said to manure the soil (1 Hectar = 40,000 □ feet) during a successional harvest of five years, contains:

| | Kilogr. |
|---|---|
| Carbon | 3637·6 |
| Hydrogen | 426·8 |
| Oxygen | 2521·5 |
| Nitrogen | 203·2 |
| Salts and Earths | 3271·9 |
| Dry Manure | 10161·0 |

(1 Kilogramme is equal to 2·138 lbs. Pr., or 2·2 lbs. English.)

c. *Composition of the Produce* (dried in a vacuum at 110° C.).

| | With the Ashes. | | | | | After Deduction of the Ashes. | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Carbon. | Hydrogen. | Oxygen. | Nitrogen. | Ashes. | Carbon. | Hydrogen. | Oxygen. | Nitrogen. |
| Wheat | 46·1 | 5·8 | 43·4 | 2·3 | 2·4 | 47·2 | 6·0 | 44·4 | 2·4 |
| Rye | 46·2 | 5·6 | 44·2 | 1·7 | 2·3 | 47·3 | 5·7 | 45·3 | 1·7 |
| Oats | 50·7 | 6·4 | 36·7 | 2·2 | 4·0 | 52·9 | 6·6 | 38·2 | 2·3 |
| Wheat Straw | 48·4 | 5·3 | 38·9 | 0·4 | 7·0 | 52·1 | 5·7 | 41·8 | 0·4 |
| Rye Straw | 49·9 | 5·6 | 40·6 | 0·3 | 3·6 | 51·8 | 5·8 | 42·1 | 0·3 |
| Oat Straw | 50·1 | 5·4 | 39·0 | 0·4 | 5·1 | 52·8 | 5·7 | 41·1 | 0·4 |
| Potatoes | 44·0 | 5·8 | 44·7 | 1·5 | 4·0 | 45·9 | 6·1 | 46·4 | 1·6 |
| Beetroot | 42·8 | 5·8 | 43·4 | 1·7 | 6·3 | 45·7 | 6·2 | 46·3 | 1·8 |
| Swedish Turnips | 42·9 | 5·5 | 42·3 | 1·7 | 7·6 | 46·3 | 6 0 | 45·9 | 1·8 |
| Topinambour | 43·9 | 5·8 | 43·3 | 1·6 | 6·0 | 46·0 | 6·2 | 46·1 | 1·7 |
| Yellow Pease | 46·5 | 6·2 | 40·0 | 4·2 | 3·1 | 48·0 | 6·4 | 41·3 | 4·3 |
| Pea Straw | 45·8 | 5·0 | 35·6 | 2·3 | 11·3 | 51·5 | 5·6 | 40·3 | 2·6 |
| Red Clover Hay | 47·4 | 5·0 | 37·8 | 2·1 | 7·7 | 51·3 | 5·4 | 41·1 | 2·2 |
| Topinambour Stalk | 45·7 | 5·4 | 45·7 | 0·4 | 2·8 | 47·0 | 5·6 | 47·0 | 0·4 |

d. *The Experiments themselves.*

First Series.

| Successive Years. | Substances. | Crop per Hectar. | Dry Harvest. | Carbon. | Hydrogen | Oxygen. | Nitrogen. | Salts and Earths. |
|---|---|---|---|---|---|---|---|---|
| | | *Kilogr.* | *Kilogr.* | *Kilogr.* | *Kilogr.* | *Kilogr.* | *Kilogr.* | *Kilogr.* |
| 1. | Potatoes | 12800 | 3085 | 1357·4 | 178·9 | 1379·0 | 46·3 | 123·4 |
| 2. | Wheat | 1343 | 1148 | 529·3 | 66·6 | 498·2 | 26·4 | 27·5 |
| | Wheat Straw | 3052 | 2258 | 1093·0 | 119·7 | 878·2 | 9·0 | 158·1 |
| 3. | Clover (Hay) | 5100 | 4029 | 1909·7 | 201·5 | 1523·0 | 84·6 | 310·2 |
| 4. | Wheat | 1659 | 1418 | 653·8 | 82·2 | 615·4 | 32·6 | 34·0 |
| | Wheat Straw | 3770 | 2790 | 1350·4 | 147·8 | 1085·3 | 11·2 | 195·3 |
| | Swedish Turnips | 9550 | 716 | 307·2 | 39·3 | 302·9 | 12·2 | 54·4 |
| 5. | Oats | 1344 | 1064 | 539·5 | 68·0 | 330·5 | 23·3 | 42·6 |
| | Oat Straw | 1800 | 1283 | 642·8 | 69·3 | 500·4 | 5·1 | 65·4 |
| | Total | 40418 | 17791 | 8383·1 | 973·3 | 7172·9 | 250·7 | 1010·9 |
| Manure applied | | 49086 | 10161 | 3637·6 | 426·8 | 2621·5 | 203·2 | 3271·9 |
| Difference | | | + 7363 | + 4747·5 | + 546·5 | + 5551·4 | + 47·5 | − 2261·0 |

## Second Series.

| Successive Years. | Substances. | Crop per Hectar. | Dry Harvest. | Carbon. | Hydrogen | Oxygen. | Nitrogen. | Salts and Earths. |
|---|---|---|---|---|---|---|---|---|
| | | *Kilogr.* | *Kilogr.* | *Kilogr.* | *Kilogr.* | *Kilogr.* | *Kilogr.* | *Kilogr.* |
| 1. | Beetroot . | 26000 | 3172 | 1357·7 | 184·0 | 1376·7 | 53·9 | 199·8 |
| 2. | Wheat . . | 1185 | 1013 | 467·0 | 58·8 | 439·6 | 23·3 | 24·3 |
| | Wheat Straw . | 2693 | 1993 | 964·0 | 105·6 | 775·3 | 8·0 | 139·5 |
| 3. | Clover (Hay) | 5100 | 4029 | 1909·7 | 201·5 | 1523·0 | 84·6 | 310·2 |
| 4. | Wheat . . | 1659 | 1418 | 653·8 | 82·2 | 615·4 | 32·6 | 34·0 |
| | Wheat Straw . | 3770 | 2790 | 1350·4 | 147·8 | 1085·3 | 11·2 | 195·3 |
| | Carrots . . | 9550 | 716 | 307·2 | 39·3 | 302·9 | 12·2 | 54·4 |
| 5. | Oats . . | 1344 | 1064 | 539·5 | 68·0 | 390·5 | 23·3 | 42·6 |
| | Oat Straw . | 1800 | 1283 | 642·8 | 69·3 | 500·4 | 5·1 | 65·4 |
| | Total . | 53101 | 17478 | 8192·7 | 956·5 | 7009·0 | 254·2 | 1065·5 |
| Manure applied . | | 49080 | 10161 | 3637·6 | 426·8 | 2621·5 | 203·2 | 3271·9 |
| Difference . . | | | + 7317 | + 4555·1 | + 529·7 | + 4387·5 | + 51·0 | − 2206·4 |

## Third Series.

| Successive Years. | Substances. | Crop per Hectar. | Dry Crop. | Carbon. | Hydrogen | Oxygen. | Nitrogen. | Salts and Earths. |
|---|---|---|---|---|---|---|---|---|
| | | *Kilogr.* | *Kilogr.* | *Kilogr.* | *Kilogr.* | *Kilogr.* | *Kilogr.* | *Kilogr.* |
| 1. | Potatoes . | 12809 | 3085 | 1357·4 | 178·9 | 1379·0 | 46·3 | 123·4 |
| 2. | Wheat . . | 1343 | 1148 | 529·3 | 66·6 | 498·2 | 26·4 | 27·5 |
| | Wheat Straw . | 3052 | 2258 | 1093·0 | 119·7 | 878·2 | 9·0 | 158·1 |
| 3. | Clover (Hay) | 5100 | 4029 | 1909·7 | 201·5 | 1523·0 | 84·6 | 310·2 |
| 4. | Wheat . . | 1659 | 1418 | 653·8 | 82·2 | 615·4 | 32·6 | 34·0 |
| | Wheat Straw . | 3770 | 2790 | 1350·4 | 147·8 | 1085·3 | 11·2 | 195·3 |
| | Swedish Turnips | 9550 | 716 | 307·2 | 39·3 | 302·9 | 12·2 | 54·4 |
| 5. | Pease . . | 1092 | 998 | 464·1 | 61·9 | 399·2 | 41·9 | 30·9 |
| | Pease Straw . | 2790 | 2461 | 1127·3 | 123·0 | 876·1 | 56·6 | 278·1 |
| 6. | Rye . . | 1679 | 1394 | 644·0 | 78·1 | 616·1 | 23·7 | 23·1 |
| | Rye Straw . | 3731 | 3033 | 1513·5 | 169·8 | 1231·4 | 9·1 | 109·2 |
| | Total . | 46566 | 23330 | 10949·7 | 1268·8 | 9404·8 | 353·6 | 1353·2 |
| Manure applied . | | 58900 | 12192 | 4364·2 | 512·2 | 3145·5 | 243·8 | 3925·8 |
| Difference . . | | | + 11138 | + 6585·5 | + 756·6 | + 6259·3 | + 109·8 | − 2572·6 |

## Fourth Series.

| Successive Years. | Substances. | Crop per Hectar. | Dry Crop. | Carbon. | Hydrogen | Oxygen. | Nitrogen. | Salts and Earths. |
|---|---|---|---|---|---|---|---|---|
| | | *Kilogr.* | *Kilogr.* | *Kilogr.* | *Kilogr.* | *Kilogr.* | *Kilogr.* | *Kilogr.* |
| 1. | Manured Fallow . . | — | — | — | — | — | — | — |
| 2. & 3. | Wheat . . | 3318 | 2836 | 1037·4 | 164·5 | 1230·8 | 65·2 | 68·1 |
| | Wheat Straw . | 7500 | 5550 | 2686·2 | 294·2 | 2159·0 | 22·2 | 388·5 |
| | Total . | 10818 | 8368 | 3993·6 | 458·7 | 3389·8 | 87·4 | 456·6 |
| Manure applied . | | 20000 | 4140 | 1284·5 | 173·9 | 1068·1 | 82·8 | 1333·1 |
| Difference . . | | | + 4246 | + 2511·5 | + 284·8 | + 2321·7 | + 4·6 | − 876·5 |

## Fifth Series.

### Cultivation of Topinambour.

| Successive Years. | Substances. | Crop per Hectar. | Dry Crop. | Carbon. | Hydrogen. | Oxygen. | Nitrogen. | Salts and Earths. |
|---|---|---|---|---|---|---|---|---|
| | | *Kilogr.* | *Kilogr.* | *Kilogr.* | *Kilogr.* | *Kilogr.* | *Kilogr.* | *Kilogr.* |
| 1. | Topinambour | 52880 | 11020 | 4763·0 | 638·0 | 4763·0 | 176·0 | 660·0 |
| 2. | Woody Stalk | 28200 | 24542 | 11224·7 | 1326·3 | 11224·7 | 98·2 | 687·2 |
| | Total . | 81080 | 35562 | 15987·7 | 1964·3 | 15987·7 | 274·2 | 1347·2 |
| | Manure applied . | 45450 | 9408 | 3368·1 | 395·1 | 2427·3 | 188·2 | 3029·3 |
| | Difference . | . | +26154 | +12619·6 | +1569·2 | +13560·4 | +86·0 | —1682·1 |

### e. *Synopsis of all the Experiments.*

| Series. | Dry Manure per One Hectar per Year. | Nitrogenous Contents of Manure. | Dry Crop in One Twelve-month. | Nitrogen of the Crop. | Gain in Organic Material. | Gain in Nitrogen. |
|---|---|---|---|---|---|---|
| | *Kilogr.* | *Kilogr.* | *Kilogr.* | *Kilogr.* | *Kilogr.* | *Kilogr.* |
| 1. | 2032 | 40·6 | 3558 | 50·1 | 1526 | 9·5 |
| 2. | 2032 | 40·6 | 3495 | 50·8 | 1463 | 10·2 |
| 3. | 2032 | 40·6 | 3888 | 58·9 | 1856 | 18·5 |
| 4. | 1360 | 25·8 | 2795 | 29·1 | 1435 | 3·3 |
| 5. | 4704 | 94·1 | 17781 | 137·1 | 13087 | 43·0 |

## II. Cultivation of Lucerne, communicated by Mr. Crud, and calculated by Boussingault.

(Lucern-hay contains, upon an average, in 100 parts, 2·35 nitrogen.)

| Cultivated Plant. | Crop per Hectar in Kilogrammes. | Nitrogen in Kilogrammes. |
|---|---|---|
| 1st year Lucern-hay . . . . | 3360 | 79 |
| 2nd „ „ . . . . | 10080 | 237 |
| 3rd „ „ . . . . . | 12500 | 294 |
| 4th „ „ . . . . . | 10080 | 237 |
| 5th „ „ . . . . . | 8000 | 188 |
| 6th „ Wheat { Corn . . . | 1580 | 31 |
| 6th „ Wheat { Straw . . . | 3976 | 12 |
| | 44000 | 1078 |
| Manure applied . . . . | | 224 |
| Excess of Nitrogen . . . . | | 854 |
| Do. do. for the year . . | | 142 |

## III. Contents in Ashes of some Cultured Plants.

| | Names of the Plants, and of the Examiners. | Salts of Potash and Soda. | Salts of Lime and Magnesia. | Phosphatic Salts. | Silica. |
|---|---|---|---|---|---|
| Siliceous Plants | Oats: Straw and Seed, (*Wiegmann & Polsdorff*) | 34·00 | 4·00 | . . | 62·00 |
| | Barley: Straw and Seed, (*Wiegmann & Polsdorff*) | 19·00 | 25·70 | . . | 55·03 |
| | Hay (*Haidlen*) . . | 5·50 | 28·60 | 21·10 | 60·10 |
| | Rye Straw (*Fresenius*) | 18·65 | 16·52 | 6·98 | 63·89 |
| | Wheat Straw (*De Saussure*) . . . | 22·00 | 7·20 | 11·20 | 61·05 |
| | Barley Straw (*De Saussure*) . . . | 20·00 (?) | 20·25 | 7·75 | 57·00 |
| Lime-Magnesia-Plants | Meadow Clover (*Wiegmann* and *Polsdorff*) . | 39·20 | 56·00 | . . | 4·90 |
| | Lucerne (*Hertwig*) . | 36·13 | 60·73 | 13·52 | 2·26 |
| | Tobacco, German, (*Hertwig*) . . | 23·07 | 62·23 | 17·95 | 15·25 |
| | Tobacco, Havanna, (*Hertwig*) . . | 24·34 | 67·44 | 9·04 | 8·30 |
| | Potato Stalks (*Berthier* and *Braconnot*) . | 4·20 | 59·40 | . . | 36·40 |
| | Potato Stalks (*Hertwig*) . . . | 6·97 | 53·17 | 9·78 | 29·81 |
| | Pea Straw (*Hertwig*) . | 27·81<br>20·05 | 61·38<br>60·08 | 11·62<br>12·61 | 7·81<br>15·54 |
| Potash-Soda-Plants | Maize Straw (*De Saussure*) . . . | 71·00 | 6·50 | 14·70 | 18·00 |
| | White Turnips (*Liebig*) | 81·60 | 18·40 | | |
| | Beet-root (*Hruschauer*) | 88·00 | 12·00 | | |
| | Potatoes (*Hruschauer*) | 85·81 | 14·19 | | |
| | Topinambour (*Braconnot*) . . | 84·30 | 15·70 | | |
| Phosphatic Plants | Wheat, red, (*Fresenius*) | 86·64 | 22·96 | 104·64(?) | 0·15 |
| | Wheat, white, (*Will*) . | 52·98 | 38·02 | 91·67 | 0·30 |
| | Rye (*Fresenius*) . . | 65·16 | 32·12 | 96·18 | 0·50 |
| | Peas (*Will*) . . | 71·50 | 24·55 | 85·46 | |
| | Large Beans (*Büchner*) | 71·54 | 28·46 | 97·05 | |
| | Maize (*De Saussure*) . | . . | . . | 83·50 | 1·00 |
| | Barley (*De Saussure*) . | . . | . . | 76·70(?) | 0·5(?) |

## IV. Proportion of Nitrogen and of Phosphoric Acid in Nutritive Plants, according to Boussingault.

| Nutritive Plants. | Constituents of Ashes. | Nitrogen. | Phosphoric Acid. |
|---|---|---|---|
| Hay | 62·33 | 11·50 | 3·57 |
| Potatoes | 9·64 | 3·70 | 1·09 |
| Beetroot | 7·70 | 2·10 | 0·46 |
| Swedish Turnips | 5·70 | 1·30 | 0·35 |
| Potatoes | 12·47 | 3·75 | 1·35 |
| Wheat | 20·51 | 20·50 | 9·64 |
| Maize | 11·00 | 16·40 | 5·51 |
| Oats | 31·74 | 17·87 | 4·73 |
| Wheat Straw | 51·90 | 3·00 | 1·61 |
| Oat Straw | 35·70 | 3·00 | 1·07 |
| Clover Hay | 73·50 | 21·00 | 4·63 |
| Peas | 30·00 | 38·40 | 9·03 |
| White Beans | 35·00 | 45·80 | 9·38 |
| Large Beans | 30·00 | 51·10 | 10·26 |

The proportion of phosphoric acid to nitrogen is here, upon an average, 1 : 3·5. The greatest deviations *in maximo* are 1 : 4·9, *in minimo* 1 : 1·9. If we omit the four greatest deviations, the average would be 1 : 3·6, and the greatest deviations are 1 : 2·8 and 1 : 4·5. We ought, however, to take into consideration that the determination of the nitrogen, but still more of the phosphoric acid, is attended with the greatest difficulty, and therefore may be still open to considerable corrections.

## V. Experiments of Kuhlmann on the Effect of Ammoniaical Manures upon the Produce of Meadows. — (*Comptes rendus, Nov.* 13, 1843.)

The experiments were instituted in the rather rainy year of 1843 ; the salts of the manure were applied on the 28th of March, and the harvest took place on the 30th of June. The following Table gives the results : —

| No. | Nature of the Manure. | Quantity per Hectar. | Crop per Hectar. | Nitrogenous Contents of the Manure. | The manured Meadow therefore delivered more than the unmanured one, as follows : |
|---|---|---|---|---|---|
| | | *Kilogr.* | *Kilogr.* | | |
| 1. | No manure | | 4000 | | |
| 2. | Sulphate of Ammonia | 266 | 5233 | 50·08 | 12·33 |
| 3. | Hydrochlorate of Ammonia | 266 | 5716 | 70·33 | 17·16 |
| 4. | Nitrate of Soda | 266 | 5723 | 44·10 | 17·63 |
| | | *Litr.* | | | |
| 5. | Urine of Horses | 21666 | 6240 | 349·27 | 22·40 |
| 6. | Ammoniacal Water from the Gas-works at Lisle | 5400 | 6300 | ? | 23·00 |
| 7. | Water from Animal Bone Mills | 21666 | 6493 | 938·14 | 24·93 |
| 8. | Flemish Manure | 21666 | 7433 | 43·22 | 34·33 |

### Observations on the Articles of Manure.

No. 6. This water was neutralised by the hydrochloric acid water of the glue manufactories, and thus a precipitate of phosphate of lime was applied to the meadow.

No. 7. The bones having been boiled in order to remove the fat, contained about 2½ per cent. of impure gelatine, with 16·98 per cent. of nitrogen. (The specific gravity I have put at 1·021. The water of course likewise contained all the insoluble salts of the bones, the vessels, skin, and sinews attached to it.)

No. 8. The Flemish manure, in this instance, consisted almost exclusively of the urine and excrement of human beings (*état normal?*): the specific gravity I assume at 1·05; the nitrogenous contents, according to Boussingault, at 0·19 per cent.

The most rapid and remarkable effects were exhibited by No. 6, 7, and 8.

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## B.

### LIST OF OLD TREES, ACCORDING TO MOQUIN-TANDON. — (*Tératologie Végétale.*)

THERE are known —

| | | |
|---|---|---|
| Palms of | 200, 300 | years. |
| Cercis | 300 | „ |
| Chirodendron | 327 | „ |
| Ulmus (Elm) | 355 | „ |
| Cupressus (Cypress) | 388 | „ |
| Hedera (Ivy) | 448 | „ |
| Acer (Maple) | 516 | „ |
| Larix (Larch) | 263, 576 | „ |
| Castanea (Chestnut) | 360, 626 | „ |
| Citrus (Oranges, Lemons, &c.) | 400, 509, 640 | „ |
| Platanus (Plane) | 720 | „ |
| Cedrus (Cedar) | 200, 800 | „ |
| Juglans (Walnut) | 900 | „ |
| Tilia (Lime) | 364, 530, 800, 825, 1076 | „ |
| Abies (Spruce) | 1200 | „ |
| Quercus (Oak) | 600, 800, 860, 1000, 1600 | „ |
| Olea (Olive) | 700, 1000, 2000 | „ |
| Taxus (Yew) | 1214, 1466, 2588, 2880 | „ |
| Schubertia | 3000, 4000 | „ |
| Leguminosæ | 2052, 4104 | „ |
| Adansonia (Baobab) | 6000 | „ |
| Dracæna (Dragon Tree) | 6000 | „ |

# C.

## CONTAINING THE NEW PASSAGES IN THE THIRD GERMAN EDITION OF THE FIRST AND SECOND BOOKS: Leipsic, 1849.

### *Page* 18., *fourth line from the bottom.*

*Development of the Starch Granule.*—In very young potatoes we find exceedingly minute granules; in general, a greater number of small than of large ones: even in the cells of old potatoes minute granules occur, mingled with the larger. If we regard the very minute granules as the rudiments of the structure, and take the different size as standard for estimating the age, the result is as follows: the smaller (therefore the younger) the granules are, the more truly spherical they appear, and the ovate or irregular outline is subsequently acquired. It is easy to see that this deviation from the original globular form is not caused by internal layers, but by the outer, the unequal thickness of which produces the gradual alteration of the outline; while the innermost layers continue to exhibit the form (spherical) which the youngest, that is, the most minute, granules present. The conclusion from this is, that the outermost layers are the youngest, and the innermost the oldest; that is to say, the starch grows by the successive deposition of new layers upon the older. The probability deduced from the investigation of the potato becomes almost certainty when we compare the starch granules in the tuberous stem of *Bletia Tankervilliæ*, in the rhizome of *Lathræa squamaria*, and in the stem of *Dieffenbachia seguine*. In *Bletia*, by far the greater part of the granules have a most characteristic outline, easy to be detected; and the structure of the layers is equally peculiar. Others are enclosed by additional layers of a totally different shape, laterally excentric from the former; and it is almost impossible to refuse the conviction that the outer layers are the last formed. The same holds good of *Dieffenbachia*, only the granules are here more difficult to observe. Fritsche arrived at the same conclusion from the consideration of the "twin-granules," enclosed by simple outer layers; and most observers have since maintained it. The only other views are the baseless and daring speculations of, in some cases, most superficial observers: these require no refutation, since they are not supported even by an appearance of probability.

### *Page* 23. § 10.

The author adopts the term *protoplasma*, proposed by Mohl, in the place of mucus (*schleim*), the name formerly given to the quaternary and proteine compounds, and which has been adopted in this translation.

*Page* 31., *substitute for* § 14.

§ 14. By the plant-cell (*cellula*) I understand exclusively the elementary organ, which, when fully developed, possesses a wall formed of cellulose and a semi-fluid nitrogenous lining, constituting the sole essential element of form of all plants, and without possessing which nothing can be called a plant (*ohne welche eine Pflanze nicht besteht*).

Cells can only be formed in a fluid which contains sugar, dextrine, and proteine compounds (*formative matter, cytoblastema*). The proteine compounds appear to be the primary producers of the process here, as in the chemical metamorphoses (§ 11.). Two points must be distinguished:

I. The formation of cells without the influence of another cell previously existing. This occurs in fluids capable of fermentation. A globule of nitrogenous substance originates; in this a cavity is formed, it grows, and the complete cell has a delicate coat of cellulose, without our being able to determine the epoch of its production.

II. Formation of cells under the influence of a complete cell already existing, or multiplication of the plant-cell. The mode of multiplication of vegetable cells does not appear to follow the same type in all cases. Apparently we may at present distinguish at least two kinds of multiplication.

1. The nitrogenous substance, the *protoplasma*, collects into a more or less perfectly spherical body, at length sharply defined, the nucleus of the cell (*cytoblastus*); upon this is deposited a layer of protoplasm, which expands as a vesicle, and forms the subsequent lining of the cell: at a very early period the whole becomes enclosed by a wall of cellulose, and the cell is completed. This appears to occur especially in the embryo-sac and the embryonal vesicle.

2. The whole contents of a cell, including the nitrogenous lining, divide into two portions, which appear to be separated by a lighter zone; and around each portion is formed a wall of cellulose. The nucleus of the cell appears to behave differently here, since:

*a.* It divides, and is thus doubled, so that each of the newly-formed nuclei becomes the central point for one of the cell-forming portions of the contents; or,

*b.* It disappears, so that a new nucleus is developed in each of the new cells *after* their production.

This mode (2.) of multiplication appears to occur in all the other parts of the plant.

This subject requires a very great deal more investigation.

I exclude from the term "cell" all hollow elementary particles of plants which do not bear the characters given in the paragraphs; and

this appears to be the only way to avoid great confusion, such as has begun to prevail in some parts of Animal Histology.

[Other work has hitherto prevented the author from resuming his researches on cell-formation in a systematic manner. He therefore gives only a few additional observations in this edition, with a short report of the labours of others.]

*Page* 33. *line* 33., *add:* —

Mohl asserts that the primordial utricle is the forerunner of the formation of the cellulose cell-wall. I have not been able to satisfy myself of this. I not unfrequently find the cell-contents of young cells wholly homogeneous, and of yellowish colour; then one or more colourless, spherical or ovate spaces originate, which expand and meet together like the bubbles in froth. On their junction, the more viscid yellowish substance is then seen to move like little currents; the bubbles gradually coalesce into a cell-cavity; the viscid fluid becomes the lining, and often circulates for some time longer. I believe, also, that I am justified in considering Mohl's primordial utricle and the circulating fluid to be perfectly identical. According to this view, the primordial utricle would be so much the more fluid the younger it was, and therefore could not be the often rather tough wall of the cell only just formed. Of course, however, an extremely delicate and not easily isolated layer of the fluid may, in a more solidified condition, form the primordial utricle, and thus the foundation of the cell.

*Page* 37., *before the History and Criticism.*

Karsten (Botanische Zeitung, 1848, p. 457, et seq.) is compelled to oppose my observations on the ferment-cells. His chief objection is: "The ferment-cells (which I must have overlooked) exist already in the uninjured fruits, and pass through the filter;" and he then concludes with a very peremptory protest against all future similar assertions. Nevertheless, after a careful repetition of my researches, I still hold provisionally to my opinion. I am quite convinced by my investigations that the utricles well known to me in certain (not in all, e. g. not in the Apple) fruits, the juice of which is capable of fermentation, have nothing at all in common with the ferment-cells I have so often examined; that the ferment-cells also certainly originate in some fruits, such as the grape, with the others, and quite independently of them, and then multiply so rapidly in the must, that I could not decide that they were not already nascent in the filtered drops; but that there is certainly an epoch for the grape, in which neither ferment-cells nor those utricles exist, notwithstanding that the juice is capable of fermentation, and developes perfectly good ferment; that especially apple-juice, which ferments so well, contains neither those utricles nor ferment-cells; that, altogether, the juices of all fruits prepared and filtered before the commencement of the formation of ferment-cells are altogether destitute of anything solid, anything organic; in fact, of any thing visible besides drops of oil. I believe that Karsten would have kept back all his objections, at least for the present, if he had combined the internal development of succulent fruits with his fermentation experiments. These peculiar utricles have to be spoken of at length in another place (§ 39. Appendix, 574, *c.*).

## *Page* 38., *add to History and Criticism.*

In conclusion, I give an as complete as possible review of the whole history of the study of vegetable cell-formation since 1838, in which year, through my work, the origin of the vegetable cell was first declared to be the fundamental problem in Botany.

A dissertation on the multiplication of the vegetable cell by division, by Hugo von Mohl, had indeed appeared earlier, in 1835, but this only bore reference to one isolated case, and a more recent revision of it will be mentioned below. In other cases, I place the researches in chronological order. I restrict myself to a brief statement of the peculiar observations and opinions of the authors, without entering upon a criticism of them, or the refutations which they have received one from another. Only I must mention that I do not go minutely into Hartig's views (Das Leben der Pflanzenzelle, Berlin, 1844), because, as Mohl has already remarked, he has such a very different way of looking at the things from us, that it is impossible to give an account of the matter without using his own words, and at equal length with himself.

1838. *Schleiden*, Beiträge zur Phytogenesis, in Müller's Archiv (Beiträge zur Botanik, p. 129.). The contents have been given at length above.

*Unger*, Aphorismen zur Anatomie u. Physiologie der Pflanzen. Vienna, 1838. Here we find a resurrection of Grew's opinion, that the cells originate as cavities in homogeneous mucilage, without independent walls. This appears to me rather speculation than observation.

*Hugo von Mohl*, On the Development of the Stomates, in the Linnæa, 1838 (Vermischte Schriften, p. 252.). An instance of multiplication of cells by the so-called division.

1839. *H. v. Mohl*, Development of the Spores of *Anchoceros lævis*, in the Linnæa, 1839 (Vermischte Schriften, p. 84.), relates the origin of transparent utricles in the mucilaginous contents of the cells, whereby the nitrogenous lining (primordial utricle) is gradually detached from the cell-contents, and at the same time, by the meeting of the utricles, becomes defined at the points of junction of the course of the little mucilage currents in cells. The nucleus of the parent-cell is persistent, and another is formed, which, by repeated division, multiplies to four, which arrange themselves tetrahedrally. Septa then divide the parent-cell into four parts, in such a manner that the nuclei lie in the middle of each subdivision. At the same time the nucleus of the parent-cell disappears. The four newly-formed cells subsequently separate, with special walls, from the parent-cell, lie free in it, and finally are emitted by the destruction of the parent-cell.

1840. *Schleiden*, Zur Anatomie der Cacteen (Mém. de l'Acad. de St. Petersbourg, 6th series.) The contents have been incorporated above.

1841. *Unger*, in the Linnæa. The nuclei are formed subsequently in the completed cell.

1842. *Nägeli*, Ueber Entwicklung des Pollens; Zürich. Describes the development of the cell around a central nucleus in the pollen granules of the *Phanerogamia.*

*Nägeli*, in the Linnæa. Development of the cells of the stomates. A small triangular mark between the two secondary cells, which have

originated in the parent-cell, is said to represent the intercellular passage between them. Endosmose of water completely isolates the two secondary cells from each other.

1843. *Quekett*, in the Microscopical Journal and Structural Record for 1841, ed. by D. Cooper (in the extract in the Botanische Zeitung, p. 80.). The primary utricles of the vessels are derived from cytoblasts, which subsequently become absorbed.

*Mirbel* and *Payen*, in the Comptes rendus, January. A globulocellular substance, the cambium, precedes the formation of cells; consists of hydrates of carbon, dextrine, gum, sugar, &c., and nitrogenous substances.

*Endlicher* and *Unger*, Grundzüge der Botanik. Distinguish primary and secondary cell-formation. The first consists in the development of cavities in an uniform mucilaginous substance. Originally the cavities have no proper walls; these are subsequently formed — particularly in Algæ, Lichens; general in the lower plants, rare in the higher. The second is either intra-utricular or merismatic cell-formation. In the former, the cells are formed, singly or in numbers, from the contents of cells already existing, so that the parent-cells expand and become dissolved; especially in the formation of spores and pollen. The latter, or merismatic cell-formation, consists in the division of existing cells by the formation of septa. This kind of cell-formation is the most general. In both the latter kinds of cell-formation it is not the nucleus from which the new cells are immediately produced, but the mucilaginous granular contents of the cell.

*Hermann Karsten*, De Cella vitali Dissertatio. The cells originate by the expansion of amorphous granules of organic matter in the cells.

1844. *Hugo von Mohl*, Some Observations on the Structure of Vegetable Cells (in the Botanische Zeitung, p. 273.). In all vitally active cells a living membrane occurs, consisting of a nitrogenous layer: this membrane exists earlier than the cell-wall formed of cellulose, and therefore Mohl calls it the "primordial utricle." The new cells probably originate by the solution of the old primordial utricle, and the formation of several new ones effected through a nucleus, which always precedes the cell-formation.

*Unger*, The Growth of Internodes considered anatomically (in the Botanische Zeitung, p. 506.). The multiplication of the cells is the result of the formation of septa. The nucleus is a secondary matter here.

*Nägeli*, Nuclei, Formation and Growth of Cells in Plants (in the Zeitschrift f. wiss. Botanik, B. I. Heft 1.). The opinions are essentially those given at pages 33, and 34 II.

1844. *Grisebach* (in Wiegmann's Archiv, 134, et seq.). The cells are multiplied by division, without cytoblasts. Appendix to this. There occur — 1. free rudiments of cells, swimming in the parent-cell; 2. frequently free secondary cells, swimming with these; 3. cells with parietal cytoblasts, i. e. perfect secondary cells. From this it is concluded that my theory of cell-formation is correct.

1845. *Anonymous*, Researches on the Cellular Structures which fill up Vessels (in the Botanische Zeitung, p. 225, et seq.). The cellular organs originate in the cavities of old vessels as vesicular protrusions of the neighbouring cells, which penetrate through the canals of the pores, while a nucleus is subsequently developed in them.

*Karl Müller*, Development of the *Charæ* (in the Botanische Zeitung, p. 410, et seq.). A fluid composed of amylum becomes agglomerated as a ball into a cytoblast; this is therefore nitrogenous, since the abundance of nitrogen in starch is well known in gluten (!!!); around the cytoblast is formed a cell.

*Karl Müller*, On the Scales of *Trichomanes membranaceum* (in the Botanische Zeitung, p. 580, et seq.). The cell-formation occurs in the known manner, through cytoblasts: this is founded on dried specimens (!).

*Hugo von Mohl*, On the Development of Stomates (in his Vermischte Schriften). Appendix. The nucleus becomes doubled by division. Then a simple septum is somewhat suddenly formed between the two, dividing the whole cell into two portions. The septum subsequently splits into two lamellæ, as a furrow penetrates it at the upper and under sides of the cells.

*Schaffner*, Some Researches on the Multiplication of Cells (in the Flora, p. 481, et seq.). Cells are formed around one or more cytoblasts, also around cytoblasts and cells already completed. The cytoblasts may also be developed independently into cells, by becoming hollow. Cells are also formed without a nucleus, the nucleus growing afterwards. Multiplication of cells by division does not occur. The very youngest cells exhibit no primordial utricle; this is subsequently formed.

*Karl Müller*, Some Observations on the Formation of Starch (in the Botanische Zeitung, p. 833, et seq.). The cytoblasts are converted into starch, and this only occurs in the completed cells. The cytoblast expands vesicularly, is metamorphosed into amylum (passes into a different condition of aggregation!!!); new layers are deposited upon the interior of its walls from the cytoblastema. The whole is observed in the fruits of rotten *Charæ*.

*Hugo von Mohl*, On the Multiplication of Vegetable Cells by Division (in his Vermischte Schriften, p. 362, et seq.). In the *Confervæ*, particularly in *Conferva glomerata*, the primordial utricle forms a circular fold inward, and thus divides the cell-contents into two portions; this fold of the primordial utricle is followed somewhat later by a fold of the cell-membrane itself, which, finally arriving at the axis of the cell, blends, and from the nature of its origin forms a complete double septum: thus one cell has become two by division.

1846. *Nägeli*, Nuclei, Formation and Growth of Cells in Plants (in the Zeitschrift für wiss. Botanik, Heft 3 and 4. p. 22, et seq.). 1. There is a free cell-formation without a nucleus, through expansion and excavation of a minute globule, in certain of the lower *Algæ*, and in the formation of the spores of the Lichens and Fungi. Sometimes a nucleus is subsequently produced in the completed cell. This process of abnormal cell-formation also occurs in the older cells of the *Confervæ*, as also in the formation of the spores in the species of *Zygnema*. 2. Perfectly homogeneous globules of mucilage are formed, the nucleoli; around these a perfectly homogeneous nucleus, on which a proper membrane is soon to be distinguished. A homogeneous layer of mucilage is deposited around the nucleus; this gradually becomes thick, especially at one side; then granular in the interior; next it is enveloped by a membrane, and the cell with a parietal nucleus is complete. This process characterises the cell-formation in the embryo-sac of the *Phanerogamia*.

*Karl Müller*, Development of the *Lycopodiaceæ* (in the Botanische

Zeitung, p. 521, et seq.). The young cells consist of a nucleus, surrounded by several concentric layers; both these and the nucleus are coloured blue by iodine. A coagulated gelatinous layer encloses the whole in the form of a cell. These cells soon disappear as amylum-cells, since they are gradually converted into a substance which becomes brown with iodine (!!!), and so forth.

1847. *Karl Müller*, Contributions to the History of Development of the Vegetable Embryo (in the Botanische Zeitung, p. 760.). The first cell of the embryo undoubtedly proceeds from the cytoblastema; the most indubitable confirmation of Schleiden's theory of cells (?).*

*Hofmeister*, Researches into the Process of Fertilisation in the *Œnothereæ* (in the Botanische Zeitung, p. 788.). The first cell in the embryonal vesicle is formed by a sudden production of a septum; consequently the most indubitable refutation of Schleiden's theory of cells (?).

## *Page* 48., *add to History and Criticism.*

The whole of Hartig's view has, moreover, been refuted by Hugo von Mohl†, in his usual profound manner, and it can scarcely be a matter for scientific discussion again. Harting‡ makes far more solid objections to Mohl's view of the gradual development of the cell-wall, and with him, in part, Mulder§, both in an anatomical and chemical point of view. Hugo von Mohl‖ refutes the opinions of both, and also answers the subsequent defence of Harting⸸ in a special treatise.¶ Harting stated that the original, yet unthickened, cell-membrane is perforated, and exhibits in its earlier conditions, when treated with iodine and sulphuric acid, a great number of white transparent pores, which subsequently become closed by the layer of deposit upon the *outer* surface of the cell-walls. On the other hand, Mohl repeats that these pores, previously seen and described by me**, are not perforations, but closed by a delicate membrane, the original membrane of the cell, which membrane also assumes a blue colour, though very light. Mohl does not mention what I have met with frequently in delicate transverse sections; for instance, in the parenchyma of the cabbage stalk, in the albuminous body of the Tagua nut (vegetable ivory), &c., that a fine streak extends between the cells, of a substance which remains almost colourless, while the cell-membrane becomes deep blue with iodine and sulphuric acid. When the section was successful, I always saw this substance separated into two portions (the original membranes of the two contiguous cells) by a delicate line. Harting further deduces, from micrometric measurements, that the cavity of the cell does not become smaller through

* This author, as his researches in *Monotropa* show, cannot even distinguish the embryo from the endosperm.

† H. v. Mohl, Observations on the Structure of the Vegetable Cell. Botanische Zeitung, 1844, p. 273.

‡ Harting, Microscopic Researches into the Walls of vegetable Cells (in Scheikondige Onderzoekingen; extract by H. v. Mohl in the Botanische Zeitung, 1846, p. 64.).

§ Mulder, Physiological Chemistry, translated by Moleschott; in English, by Fromberg.

‖ H. v. Mohl, On the Growth of Cell-membrane. Bot. Zeit. 1846, p. 337.

⸸ Harting, Letter to H. v. Mohl, &c. Bot. Zeit. 1847, p. 337.

¶ H. v. Mohl, Investigation of the Question, Is Cellulose the Element of all Vegetable Membranes? Bot. Zeit. 1847, p. 497.

** Wiegmann's Archiv, 1838, vol. i. p. 49.; Beitr. z. Botanik, vol. i. p. 16.

the thickening; therefore the layers of thickening must be deposited on the outside. This objection again is refuted by H. v. Mohl, by the help of most accurate measurements and acute reasoning. The third point refers to chemical relations. They are as follows:—The entire wall of the young cell re-acts purely as cellulose, for, treated with iodine and sulphuric acid, it becomes blue throughout its entire thickness. The older cells exhibit various layers. The most external consist of a matter quite insoluble in sulphuric acid. This membrane is therefore deposited externally upon the original cellulose layer, and closes up the original pores at the outside. The remainder of the layers acquire a colour less blue and more green and yellow in proportion as they lie more externally; wherefrom Mulder deduces either a disappearance of the cellulose and replacement by new substance, or a deposition of new layers always on the outside of the preceding. Harting, on the contrary, finds in this a proof that the originally pure cellulose becomes subsequently saturated with an incrusting (proteinous) substance, which accumulates especially in the outer parts. In opposition to these, Hugo von Mohl demonstrates that, in the first place, the results deduced from chemical relations are not conclusive; and, secondly, that all membranes in the entire plant, all so-called intercellular substance, and the secreted layer of the epidermis, have cellulose for their element, and are only brought to re-act differently to iodine and sulphuric acid by a gradual and varying degree of saturation by a foreign matter which penetrates them; that this inter-penetrating substance may be removed from all the parts forming the external coverings of plants, e. g. the secreted layers of the epidermis, cork and bark, by action of caustic potash, or from all the internal greatly thickened elements of the plant, e. g. pith, wood, and liber-cells, by boiling in nitric acid; a single exception occurring in a very delicate lamella on the secreted layer of the epidermis, which remains of a yellow colour under all circumstances, and therefore Mohl wishes the term *cuticula* to apply exclusively to this lamella.

In conclusion, I will only observe, that from my own researches I must accede to these results of Mohl's in every respect.

*Page* 92., *add before* § 40.

*c.* At the period of complete maturation occur in the cells of succulent fruits, the grape, gooseberry, many kinds of *Solanum*, &c., numerous more or less minute spherical vesicles of extreme delicacy, the walls of which consist of a slightly granular protoplasma, the contents of a watery, and often coloured, juice. So far as I could see, they originate at once of full size, as vesicles or bubbles of the primordial utricle, upon which they are at first flatly applied. Subsequently they separate by constriction. Hartig*, who mixes them up with many other things, calls them *metacardial* cells. Karsten† confounds them with the ferment-cells. Nägeli‡ enumerates them in part under his abnormal cell-formation. I regard them as altogether dependant forms, incapable of further development.

* Das Leben der Pflanzenzelle: Berlin, 1844.
† Creation (*Die Urzeugung*), Botanische Zeitung, 1848, p. 457.
‡ Zeitschrift für wiss. Bot., vols. iii. and iv. (1846), p. 23, et seq.

*Page* 97., *add at line* 3.

We have recently received an excellent treatise on the origin of these motions, from H. v. Mohl (On the Motion of the Sap in the Interior of the Cell. Botanische Zeitung, 1846, p. 73.). He demonstrates how several cavities filled with watery fluid are gradually formed in the young cell, originally filled with homogeneous protoplasma; how these cavities expand, by degrees meet, and thus at last displace the protoplasma to such an extent that it only forms a thin layer on the internal surface of the cell, with thickened places in it, filaments as it were, some of which run across the cell; while the motion simultaneously commences in all these filaments, or perhaps now first becomes visible through granules beginning to appear in the originally homogeneous protoplasma. I can wholly confirm this account.

*Page* 104., *add to line* 17.

Hugo Mohl, in a revision of his first treatise*, has placed the matter beyond all doubt. See Appendix, page 572, line 30.

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## D.

### ON THE USE OF THE MICROSCOPE IN BOTANICAL INVESTIGATIONS.

Considering the experience of the last thirty years, there is no need to observe that a profound study of any of the natural sciences, and especially of organisation, is impossible without the aid of the microscope. He who expects to become a botanist or a zoologist without using the microscope, is, to say the least of him, as great a fool as he who wishes to study the heavens without a telescope. I will therefore say no more respecting the value of this instrument. But as yet there has been no satisfactory work on its use, owing to the deficiency of a proper theory of vision itself. I will therefore attempt to give some indications in this respect.

The conception of distance is the result of a mathematical judgment. We must consider accurately the conditions connected with the simplest cases. We take up images on the retina at first as luminous points, and afterwards as planes, situated beyond us. The lines on the different points of this surface form angles among themselves, and these angles, in various directions, are next apprehended. But it is evident that these angles differ according to the different distances of these various points from the eye. All relative determinations of size must, therefore, first be mathematically constructed, the starting-point of which is evidently the size of the angle of vision. The second element would be the distance, of which also we become gradually conscious through comparison of many impressions, the angle of vision being again the simple foundation for this; since we generally place things at a greater distance when they appear to us under

* On the Multiplication of Vegetable Cells by Division. Verm. Schrift., 1845, p. 362.

a smaller angle of vision, and thus add distinctness to them; for we naturally feel that our eye can see nearer objects more distinctly than distant ones, owing to its having its sensibility diminished through the strata of air that intervene between distant objects. We shall find, however, on considering the physical conditions of vision, that a minimum must exist with regard to nearness, within the boundary of which distinct vision becomes impossible, because the image of the luminous point falls behind the retina.

On examining all the other means by which we judge of the bulk of objects, we shall find that we determine their relative size according to the angle of vision if they are presented to us with an equal degree of distinctness, or according to the distinctness where the visual angle is the same. In order to let an object appear larger, we therefore only need to approximate it to the eye: by this the angle of vision becomes enlarged, and the individual points of the body are removed further from each other, so that we distinguish more points in the same object than was previously possible; since two points which form an angle of vision below 40° cannot be distinguished as separate. There is, however, a limit to this in the refracting media of the eye, which amounts, on an average, to 8°. Near objects are not seen perfectly distinct, because the rays issuing from each point diverge too much to allow of their uniting in one on the retina. But it is a well-known fact that the divergent rays which issue from the focus of a lens become parallel after their passage through the same; it is further known that rays falling parallel upon a lens furnish an accurate image of a luminous point within the focal distance of the lens. If, therefore, we place a lens between our eye and the object, which we have approximated too near to the eye, in such a manner that the object is placed exactly in the focus of the lens, the rays proceeding from it will become parallel by passing through the lens, and, as such, falling upon the eye, will be concentrated on our retina with perfect distinctness. Since, then, the determination of size by the angle of vision depends, where equal distinctness exists, on the nearness of the object to the eye, the body in question will appear magnified to us, as we are enabled to distinguish a greater number of distinct points than before. This is the theory of the Simple Microscope, of the pocket lens, &c. The amount of magnifying power will depend on the nearness of the object: the nearer the object, the shorter must be the focal distance of the lens, by which the rays issuing from it are made parallel; or, as it has been said, the shorter the focal distance of the lens, the greater its magnifying power. Since the central angle on the same chord bears nearly an inverse proportion to the radius of the circle to which it belongs, the angle of vision at a distance of 4° from the eye will be twice as large as at a distance of 8°, &c.; and we may obtain the apparent enlargement by dividing the focal distance of the lens at the point of distinct vision by 8°. The degree of magnifying power, therefore, in the simple microscope, depends on the proximity of the object to the eye, as the lens only serves the purpose of rendering vision possible so near to the object. The impossibility of placing a lens between the object and our eye, when we have arrived at a certain proximity, very soon shows us the limits of our magnifying power. But we may obtain aid in another manner. It is a well-known fact in physics, that a magnified image is created, under certain conditions, by objects placed behind the lens. The image will correspond very exactly with the object if the lens is well made, and many points will be represented in the latter which, at the distance of distinct vision, would appear under a smaller angle of vision than 40″. This image may again be treated as an object, and be observed and magnified through a simple microscope as long as there appear simple points and lines capable of being resolved into two or more. This is the theory of the Compound Microscope, in which we observe the object or image formed by one lens (the object-glass), with another lens, (the eye-piece). These two instruments, the simple and compound microscope, are the only two of scientific value. The so-called solar microscope, or others constructed upon the same principles, but illumined by a different light, the oxy-hydrogen microscope, are nothing more than playthings — a somewhat enlarged magic-lantern. The object can never be so strongly magnified, nor with so much strictness and distinctness, by such an instrument as by a simple microscope: the physical conditions them-

selves involve this. The million-fold powers blazoned forth by quackery are nothing more than the most absurd statements of cubical enlargement, and are calculated by the distance of the lens from the surface which receives the image, in the same way as in the magic-lantern, and by which all accuracy of definition—the very thing requisite in scientific researches—is lost.

As a matter of course, we may mention that concave mirrors may be employed instead of transparent lenses, in the same way as in the telescope: this was first done by Amici, of Modena, and at a time when the aplanatic lens was not discovered it certainly was a very desirable improvement. This arrangement, however, has almost entirely lost its value at the present time, for, independently of the difficulty of always keeping the glass or mirror perfectly clean, it can only be made use of to afford a very low magnifying power, as otherwise the object could not be placed, and thus the greater portion of the magnifying power has always to be performed by the eye-piece, and which is liable to errors of spherical aberration in a much higher degree than is the case with the dioptrical instrument.

It is evident, from the representation we have just given, that the excellence of the microscope depends principally on the good quality of the lenses, and, in the compound microscope especially, on the correctness and definition of the object-glass, since every error belonging to the image is still more magnified through the eye-piece. There were two errors particularly which have been only recently remedied, but that with great success, namely, the chromatic and the spherical aberration, which are now removed, the former by achromatic lenses, and the latter, in simple microscopes, by Wollaston's or Chevalier's doublets; in the compound microscopes by aplanatic object-glasses. The instrument also, in which the eye-piece removes the spherical aberration by means of aplanatism, is very excellent. I do not think that much more can be seen by any microscope now manufactured in Europe, than by the combination of the three strongest object-glasses with the aplanatic eye-piece of Plössl's microscope, although it only gives a two-hundred linear magnifying power. The dimensions in the stronger powers of the same artist, in which the aplanatic eye-piece is not used, are certainly more considerable, but we do not distinguish more points or lines in the image, and therefore we do not see *more*, but only rather more conveniently. It follows, from the preceding explanations, that we should only use instruments furnished with achromatic doublets in the simple microscopes, and in compound microscopes furnished with achromatic, or at least with aplanatic, object-glasses, in order to obtain results as much as possible free from optical errors. Schiek in Berlin, and Plössl in Vienna, undoubtedly furnish the best instruments at the present time. Plössl's instruments are pretty nearly on an equality with Schiek's in all combinations in which the strongest object-glass does not occur. On the other hand, all combinations with the three strongest object-glasses are certainly to be preferred, and form the best instrument that has as yet come under my observation. The brass work is undoubtedly better in Schiek's instruments. Next to the instruments of those distinguished artists, we may probably name the more recent instruments of Pistor and Hirschmann in Berlin, of Oberhäuser and Chevalier in Paris; of the latter I have certainly not seen any, but infer as much from the results obtained through them by the French. The more recent English instruments seem to be so much inferior to those we have mentioned, that they bear no comparison. I likewise have not seen any of these, but there certainly is no lack of clever observers in England; and since, therefore, no microscopical botanical researches of any importance have been very recently furnished by England, excepting those of Robert Brown, and since what observations the English have made can frequently be easily refuted by a cursory glance through our glasses, this deficiency can only be attributed to the defectiveness of their instruments.*

* I should not, I think, be doing justice to my countrymen were I to allow the above remarks to pass without comment. Since the time the above was written, many improvements have taken place in the construction of the microscope, and in no country in Europe have so many of these been made as in England. Even at the time the

We have still to answer the question, Whether the simple or the compound microscope is preferable for scientific investigations? I must decidedly declare myself in favour of the latter, and that from the following reasons. *Ceteris paribus*, the simple microscope injures the eye much more than the compound, because the strength of the light (which is quite independent of the strength and clearness of the image, and ought to be clearly distinguished) is more intense, and strikes a smaller portion of the retina, and therefore causes a greater inequality in the excitement of the optic nerve; secondly, on account of the great inconvenience of the very short focal distance in higher powers; thirdly, because we can obtain higher powers, with the same mathematical accuracy, through the compound; and, lastly, because all the objections which were formerly urged against the compound microscope have been removed. Habit will also do much; but on comparing the observations of the last twenty years, it must undoubtedly be admitted that the discoveries and observations which have advanced science have been made by the compound microscope, with the exception of those of Robert Brown—of a man who, because he is perfectly *sui generis*, and has not his equal, should not be compared with ordinary observers. Thus much with regard to the value of the instrument. Previously, however, to proceeding to the method of observation, I must touch upon two points demanding careful consideration, because they frequently exercise great influence on scientific results, namely, the measurement and the illumination of objects.

*a.* The determination of the magnifying power of a microscope was of much greater importance in former times, before we possessed a suitable apparatus for determining directly the size of microscopical objects, than now. Formerly they divided the apparent diameter of the object by the number of the magnifying power, and thus discovered the size of the object itself. This mode of proceeding is, of course, too primitive to have any scientific value, and has consequently been abolished long ago. Nevertheless, it is of great interest to know, in many cases, of what degree the magnifying power is of which we avail ourselves. Good opticians generally attach an index to their instruments* for the magnifying power of the different combinations. But as considerable errors will occasionally be made by them, it is necessary that the observer himself should be able to ascertain the magnifying power of his instrument. This is attended with no great difficulty with regard to the simple microscope; it is also easy, after some practice, with the compound microscope. All that is required for it is a measure inscribed in black on ivory, or on very white paper, which gives lines, and a glass micrometer, which contains the same lines divided into optional parts (if intended for a very strong magnifying power, into at least sixty). The glass micrometer is then laid under the microscope, and on arranging it so that the divided lines may be seen distinctly, the measure is laid on the stage of the microscope. On looking now with one eye through the microscope, with the other on the measure beside it, which in most of the newer instruments will be within the distinct range of sight, owing to the length of the tube, both measures may be compared the one with the other, which, after some practice, is very easy: thus, if we have

author wrote (1845), instruments had been made by the great English makers, Ross, Powell, and Smith, which have certainly never been surpassed, if they have been equalled, by continental makers. Dr. Schleiden's observation on English observers is, I fear, the reverse of the truth: we have plenty of microscopes, and those the best in the world; but we have had but few observers. Our microscopes have been used rather as playthings than as the instruments of profound philosophical research. Let us hope, however, that this reproach will soon be wiped away. Already, through the efforts of the Microscopical Society of London, which was founded in 1839 to cultivate a branch of scientific inquiry which the older societies neglected to encourage, improvements in the microscope have been made, and a knowledge of its powers and mechanical arrangement diffused, which are bearing fruits not only in its own transactions, but in the transactions of some of our other scientific societies. Those who would wish to study the history of the microscope, and all that relates to it, I must refer to the admirable treatise on the microscope, by Mr. John Quekett, secretary to the Microscopical Society.—TRANSLATOR.

* Schiek's statements are generally very accurate; Plössl's, however, are almost all erroneous, and, it may be said to his honour, almost all too low.

$\frac{1}{60}$ decimal line to a quarter of an inch, we have a magnifying power of seventy-five times, &c. The methods suggested by Jacquin* and by Chevalier† are more tedious, without affording more accurate results to the practised observer. On the application of a very high magnifying power, it does not indeed matter about an error of ten per cent. It is not of much consequence whether an instrument magnifies 400 or 440 times, since an essential difference in the result is only obtained when the power is increased at least by one half.

It is a matter of course, that all magnifying powers should be stated only in terms of linear enlargement (enlargement of the diameter). It is quite an unnecessary proceeding to state the superficial enlargement, because it must be again reduced to the square root before a clear idea of the matter can be obtained. It is only quackery, desirous of deceiving the ignorant, that employs measurements of the magnifying power according to the cubical contents, and by which are obtained full-sounding millions. The thing is altogether a monstrous absurdity, as we cannot embrace the third dimension of space, either by the naked eye or by the microscope, for, in fact, we do not see bodies, but only luminous surfaces.

The highest magnifying powers which have hitherto been obtained by the most distinguished opticians, by Amici, Chevalier, Pistor, Schiek, and Plössl, do not exceed 2400—3000 diameters. But they are only scientifically available to about one third of that, say 1000—1200 diameters. If any one should assert that he had seen anything magnified 3000 diameters that could not be seen at a much lower magnifying power, it may safely be pronounced to be mere imagination. I have had an opportunity of comparing the most remarkable modern microscopes, and possess the best instruments that were ever made by Schiek, Plössl, Amici and Nobert, and am tolerably conversant with their use; but I maintain that although every thing one wishes to see can be seen with a magnifying power of 3000 diameters, yet too great a loss of light occurs, and no single line can be seen with due accuracy and precision. The reason of this is obvious. The magnifying power in all the microscopes is only gained as far as 280—300 diameters, through the object-glass. Hence we obtain the remaining enlargement through the eye-piece, but which only magnifies the image subject, as it always is, even if the object-glasses be ever so well finished, to a certain amount of spherical and chromatic aberration, and thus increases these errors in a rapidly increasing proportion. To this must be added, that the condenser of the eye-piece (collectivglas des oculars) must be omitted on account of the diminution of light which takes place in very high powers, and this not only increases, to a tenfold degree at least, the errors of the image of the object-glass, but also the very considerable errors (in consequence of the smallness of the lenses) of the eye-piece. It is a very general notion that expensive instruments are requisite for microscopical researches, and therefore only attainable by a few. But this is a most erroneous prejudice. Owing to the progress of the optical art, very useful instruments may be obtained at comparatively reasonable prices, from almost any respectable optician; and none, even among the youngest of our contemporaries, will live to see the moment when nothing further can be secured for science by the aid of such an instrument. He, however, who wishes to make original researches on the more difficult questions connected with the elementary structure of plants, must certainly provide himself with the best and most accurate instruments. It is not every one who is destined *to advance the science considerably*, but every one has a right *to make himself master of the science as it at present exists;* nor does the investigation of the elementary structure constitute by any means the whole of the science, for although very essential, yet it is but a very small part of it. The value of high magnifying powers is overrated by most, and frequently we only need a low magnifying power, particularly if we wish only to convince ourselves of the correctness of things discovered, described and delineated, by others. It is the same here as in perspective. A spire, for instance, which first of all could not be discovered

* Baumgärtner, Natur-Lehre, Supplement. Vienna, 1831, p. 636.

† Ch. Chevalier, Des Microscopes et de leur Usage, &c., p. 146.

by the naked eye, is readily and distinctly recognised as soon as it has been made out by the telescope. On the same principle, it only requires a very low magnifying power (perhaps 100 times) in order to be perfectly convinced of most facts in the anatomy of plants. The very high magnifying powers are, to a great extent, useless for morphological researches, and, with respect to these, there is still so productive and so little cultivated a field of investigation before us, that we may safely promise scientific immortality to any one who undertakes such researches with sincere industry and honest zeal, even with the most simple instruments. There is so much to be done in this department, that it would be difficult to avoid discovering something new. Skill in the preparation of objects, practice, and natural talent, are here of much greater importance than expensive instruments. I would here particularly draw attention to the pocket microscopes, which are now manufactured by Dr. Körner, in Jena. They are packed in a little case, the cover of which serves as a stand. The moveable stage is furnished with a screw for the purpose of affixing it during the preparation of an object, and with a round plate of glass, in order to moderate the light from below, or to arrest it altogether. In a moveable arm, four double lenses may be placed, which afford a clear and beautiful magnifying power of 15—120 diameters. This instrument is quite sufficient for all entomological, pharmacognostical, and botanical researches, and even for perfecting satisfactory anatomical observations. This instrument, with case and apparatus, only costs three Friedricsd'or, or seventeen dollars Prussian currency [about 2*l.* 10*s.* sterling], which would unquestionably be better laid out than if we were to purchase *hay* with it, or, in other words, 300 or 400 specimens of dry plants.*

The determination of the absolute size of very small *objects* is far more important than the determination of the magnifying power of the microscope. Accurate observers, long ago, sought for means to accomplish this; Leeuwenhoek, for instance, used clean grains of sand: having first ascertained how many of them went to a line, he strewed them among the microscopic objects, and thus determined the size of the latter by comparison. Other small substances, for instance, *pollen*, were subsequently used for this purpose. After the discovery of the transverse striæ upon the muscles, they were recommended for the same purpose, likewise the blood-globules of different animals. But all these experiments are of little value in a scientific point of view. The production of real microscopical measuring instruments was, therefore, early thought of. The oldest of them was the so called glass micrometer, namely a smooth little plate of glass, in which very fine divisions were cut by a diamond. Dollond especially distinguished himself by the manufacture of excellent and accurately finished micrometers. Within a more recent period they have been made by all good opticians. Chevalier manufactures micrometers in which the millimeter is divided into 500 parts, or the line into about 1000 parts. But these micrometers have nevertheless, some important drawbacks. Even with the best diamond, the splintering of the edges of the drawn lines can scarcely be avoided. In many cases, also, a glass-micrometer is not available at all. It is impossible, with very small objects, or with very high magnifying power, to keep the object and the divisional lines of the micrometer simultaneously within the same focus, which renders an accurate measurement almost impracticable. Objects also, which must necessarily lie in the water, in order that they may be brought under the microscope, cannot well be measured by the glass micrometer, as the small divided lines are filled up with water, and are thus rendered almost invisible.

The screw micrometer, which was first applied by Frauenhofer, is now made use of for all real scientific researches, and is generally provided with all the larger

* I am not aware that a good working microscope could be obtained in England at the above price; but a very serviceable instrument may be obtained of any of our great makers at a moderate sum compared with the price given for the highest powers, accompanied by the complicated accessories of a complete apparatus. It should be recollected that Ehrenberg, with a thirty-shilling microscope, produced his great work on the Infusoria, — a work with which British microscopy has nothing to compare, although it has spent thousands of pounds annually on its instruments.—Translator.

instruments of the German opticians. The whole instrument is based upon a contrivance which enables one to carry the object to be measured through the field of the microscope by a continuous movement in a right line, and to measure the distance performed. A moveable stage is constructed for this purpose, which consists of a plate moveable within grooves. A screw is attached to this plate, by the turning of which it is moved backwards and forwards. This screw is very accurately made of steel, and usually has 100 turns to an inch: such a screw is called a micrometer screw. Each entire turning of the screw, therefore, moves the stage forward at 0·01″. Provided the turning of the screw is perfectly uniform, the stage is moved forwards 0·0001 at each 1-100th part of a turn. In order to determine these parts, a disc divided into 100 parts is attached to one end of the screw, and likewise a fixed index, in which the number of the divisional parts may be read; finally, there is also a nonius besides the index, which enables us to determine the 10th part of the 100th part of a turn; therefore altogether 0·000001″. The measurement by this instrument is effected in the following manner. A fine cobweb-thread is fixed across the diaphragm of the eye-piece, and the screw-micrometer being placed upon the stage of the microscope, the eye-piece is turned in such a manner that the cobweb crosses the axis of the screw rectangularly. The object to be measured is then laid upon the plate of the micrometer in such a manner that one of its edges exactly touches the thread in the diaphragm; and the object, by the movement of the screw, is then cautiously carried through the field of vision until the thread touches the other edge of the object. On having accurately observed the position of the divided disc at the commencement and end of this operation, the difference of both will exactly give the diameter of the object to the 100,000th part of an inch. It is somewhat difficult during this operation to bring the object exactly into the right position. Some further contrivances are connected with the micrometer, in order to facilitate this. First of all, another plate is laid upon the plate, moveable in the direction of the axis of the screw, which additional plate is also moveable by a screw in a rectangular direction upon the former. A disc is likewise attached to the additional plate, which can be turned exactly round its axis. The placing of the object is thus facilitated. Much controversy has arisen with regard to the advantages of the screw micrometer. Its fault is principally this, that a screw can hardly ever be so accurate as to render its turnings equal among one another, and each single turning uniform in itself. On that account, many have given the preference to the glass micrometer; but this is only owing to a want of knowledge of the manner in which the glass micrometer is manufactured. I have already enumerated the defects peculiar to this instrument. To these must be added all the faults of the screw micrometer, for the production of a glass micrometer is only possible by means of a micrometer screw, which forms the lines. In addition to this, there is this disadvantage in the glass micrometer, that it only represents a very small part of the micrometer screw, and, as it may happen, perhaps the most inaccurate one, whilst the screw micrometer, enables us to repeat the measurement with different parts of the screw, and therefore it puts us in a position to rectify errors by taking an average of measurements; and indeed, at the best, there is a limit to the value of these measurements. It only needs intercourse with a practical optician to know the limits of accuracy in these instruments. A single measurement has, therefore, no value at all; for if we determine with it the breadth of an object at one 10,000th part of an inch, it may in reality be quite as likely to be one 7,000th or one 14,000th. The average, however, from three or four measurements, at different parts of the screw, gives us something like an accurate result. But comparative measurements are always the safest for scientific purposes, namely, measuring at the same time, with the same instrument, a well-known, readily attainable object, which is every where of an equal size, for instance, the blood-globules of a certain animal,—so that the statement of the size becomes, as it were, the rule to which every one may reduce the results arrived at with his instrument.*

*b*. Much depends on the illumination of objects. The more intense the light is

* For more detailed observations on micrometry, see Quekett's valuable work on the microscope.—Trans.

which issues from an object, the less is the loss which the light experiences in its passage through so many media, partly by reflection at the surfaces, partly by absorption in the interior. Two methods of using the microscope must here be distinguished — the examination of opaque and transparent objects.

The first is the oldest, most simple, and natural method. It corresponds with the manner in which we view objects with the naked eye by means of the light diffused about them. Mere daylight usually suffices for this, if the magnifying power is not very great; but if the magnifying power is high, the light (which in that case had best be artificial) is passed through a lens, or what is called Selligué's prism*, and concentrated upon the object. The examination with transparent light is very different. It is remarkable that no natural philosopher has as yet presented us with a theory of this manner of seeing; indeed, the essential difference in the two modes of observation has not even been indicated in any of the works on physics which I have read. It seldom occurs to us in ordinary life except when observing air-bubbles or other irregularities, or slightly cut designs in glass. The whole act of seeing here is founded on the different reflection or absorption of the rays of light through unequally refracting and unequally dense media in close proximity. The more powerfully refracting or denser parts permit fewer rays of light to pass through them and arrive at the eye, and appear, therefore, darker than the others. Indeed, it is very possible that two substances lying near to each other, having equal densities and equal refractive power, and therefore not to be recognised as different under the microscope, may exhibit an evident difference through the circumstance of their having a different polarising or depolarising effect upon light. The result, therefore, would always depend on the greater or less quantity of light which passes through the object from below. We must, however, take into consideration that a different quantity of light is reflected according to the angle of incidence and the direction of the rays of light coming from below.

The usual contrivance in all microscopes is a mirror, moveable in all directions, under the stage of the microscope. It is made either plane or concave, and the latter is used in order that the pencil of light proceeding from it may exactly fill up the opening in the stage; and a greater quantity of light is also obtained in this case. The best and most usual plan is to have both a plane and concave mirror, turned with their backs to each other, in the same frame, so that they may be alternated or changed at pleasure. If anything, the illumination by the plane mirror is preferable; the quantity of light is certainly not so great, but the parallelism is decidedly of greater advantage for accuracy of observation. It does not seem improbable that a distortion may take place in the image, through the convergence of the rays in the concave mirror. My attention has often been drawn to these phenomena; but I confess that I know little about it, as the opticians leave us perfectly in the dark on this point. According to Wollaston, a converging lens may be appropriately used in the simple microscope if a greater quantity of light is required.

During the examination of delicate objects, it is, however, not unfrequently the case that we are obliged to moderate the amount of light. The eye is too much irritated by a strong light, when observing very transparent objects, to be able to perceive slight or delicate differences, which are more readily perceived with less light. For this purpose the plain mirror may be covered with a small piece of white wood, ivory, or ebony, or it may be placed in such a manner that it sends no rays upon the object. There is a peculiar contrivance in the stage of all well-constructed microscopes, which serves as well to moderate the light as to allow it to fall obliquely on the object. This contrivance consists of a disc, perforated with holes of different sizes, which is attached under the stage in such a manner that the light may be made to pass at will through one of the holes, or it may even be excluded altogether. On placing this disc, which ought to be very easily moveable, in such a manner that only a part of a hole meets at one side the section of the stage, it will give us an oblique light. This contrivance (called a diaphragm) is almost indispensable. We can only get rid of a great number of illusions by a continual change of the light. An attentive observer will soon

* A prism with two convex surfaces.

see, by the shadow consequent on changing the illumination, whether a body is concave or elevated, or whether a small body is solid or hollow. But there are numerous other cases, which prove the great advantage to be derived from a proper use of various forms of illumination. Great weight has justly been always placed upon the regulation of the illumination in the microscope; and although many precautionary measures formerly employed, and the frequently very complicated apparatus, have been rendered partly superfluous in modern times through the great improvements of the optical part of the microscope; for instance, in the use of achromatic and aplanatic lenses; yet there still remains one point which deserves great attention, and the importance of which has been very much neglected by many microscopical observers. The principle laid down by Wollaston, that all light which does not immediately subserve the purpose of illuminating the object is injurious to the distinctness of vision, is a sound principle for guiding our observations at the present day. It is particularly to be recommended that all lateral light should be excluded from the eyes by a suitable screen, and with transparent objects; that all side-light should be excluded from the object by means of a hollow pasteboard tube, blackened inside, reaching from the body of the microscope to the table.

In the next place, I will make a few remarks on *the method of microscopical investigation.* The object of all microscopical investigations is to obtain as perfect a knowledge of forms and processes, which, from the dimension of the object, are invisible to the naked eye, as would be possible were the objects possessed of dimensions equal to those of substances which we can with perfect distinctness recognise by means of the naked eye. Our eye is in itself an optical contrivance; the microscope repeats nearly the same means; and we should therefore remember that the microscope can in no way give us new qualities any more than the eye itself. The function of the eye is to transmit directly to our perception variously coloured and illuminated points, which are arranged in a mathematical picture upon a plane surface, and we become conscious of the corporeal quality, the third dimension of space, by a subsequent process of the mind. We must therefore keep in view the fact, that the mode of action of the eye—we mean, of course, of the healthy eye—is founded, like that of the microscope, upon immutable mathematical laws; that errors consequently are only committed by the erring judgment in all observations, whether instituted with the naked eye or the microscope. The healthy sense and the optical in strument are always right. "Nature does all things well: confusion is only found in the heads of men." We mention this in order to allude to two very common prejudices, the influence of which upon science has been injurious in many respects, because they prevent people from tracing error to its proper source.

One of these consists in the vague phrase, that microscopical researches can never be depended upon, inasmuch as the microscope is frequently very deceptive. Such an expression, alas! has been employed within a very recent period by men who are looked up to as authorities in the natural sciences. It is easy to refute this notion. The microscope is perfectly innocent of every thing of which it is accused. The evil spirits which, as long as the world has existed, have always impeded the advances of the human mind, and which, even at the present day, and especially in the natural sciences, and still more in microscopical researches, have caused so much mischief, are precipitation, superficiality, and we may add to these scientific dishonesty, of which frivolousness is always guilty. These give us occasion, with much justice, to be upon our guard when microscopical researches are put forth; but this is not due to the falseness of the instrument, but to the untruth of men. How many persons, for instance, have given erroneous impressions by attributing the colours due to chromatic aberration to bodies, by describing air-bubbles as objects, &c.; but this is not the fault of the microscope, but of the stupidity, and the want of judgment arising therefrom, of people who make researches with an instrument of whose laws and mode of action they are ignorant, and gave their opinions about subjects of which a little reflection would have taught them that they were not in the slightest degree qualified to judge.

The other prejudice is the direct opposite of the preceding, and yet it is

frequently expressed by the same individuals, but in a concealed form. It is supposed that nothing more is requisite for microscopical investigation than a good instrument and an object, and that it is only necessary to keep the eye over the eye-piece, in order to be *au fait*. Link expresses this opinion in the preface to his phytotomical plates : " I have generally left altogether the observation to my artist, Herr Schmidt, and the unprejudiced mind of this observer, who is totally unacquainted with any of the theories of botany, guarantees the correctness of the drawings." The result of such absurdity is, that Link's phytotomical plates are perfectly useless; and, in spite of his celebrated name, we are compelled to warn every beginner from using them, in order that he may not be confused by false views. Link might just as well have asked a child about the apparent distance of the moon, expecting a correct opinion on account of the child's unprejudiced views. Just as we only gradually learn to see with the naked eye in our infancy, and often experience unavoidable illusions, such as that connected with the size of the rising moon, so we must first gradually learn to see through the medium of the microscope, and the more so as the latter is a much more difficult instrument than our eye, owing to the isolation of the objects, and of the absence of the possibility of comparison, as also on account of the necessity that compels us to exclude the use of one eye. We can only succeed *gradually* in bringing a clear conception before our mind of that which we have physiologically seen ; and just as it is easier for us to put ourselves right in a foggy day, or in a moon-illumined region, if we have already frequented the spots where they occur under other kinds of illumination, and are accurately acquainted with their separate parts, so it will be only possible for a man to make useful microscopical observations, who has not only made himself perfectly familiar with science in general, but has also paid especial attention to the particular objects which he subjects to his examination. It is in consequence of these prejudices that microscopical discoveries progress so slowly, and that they are generally only admitted in science long after their announcement. For most observers desire to see at a glance what has been done by others, and do not consider that it frequently requires years of most active research before an accurate result can be obtained, and that, even after it has been found, that it may require weeks of study before we are able to follow the course traced out by the hand of a master. Hence have arisen the many silly objections made to that greatest of microscopical observers, Ehrenberg.

The above observations will not only enable us to trace the two injurious prejudices which impede the proper use of the microscope to their source, but we may also deduce from them the leading principles which should guide us in microscopical researches.

First of all, we must once more compare the impression of light derived from the microscope, with the act of seeing by our eye. The eye, as already observed, only gives us the perception of a luminous or coloured surface. This impression, however, could scarcely be called by us a sight of the corporeal world, if we (as is the case with simple elementary observations) only saw with one eye. But, firstly, our eye is moveable, and we may wander about with it among the objects. Whilst our rolling eye passes over a number of objects, they produce different impressions on our retina at each successive moment, and each successive impression falls upon different parts of the retina. Secondly, we do not see with one eye alone, but with two. There belongs, as it were, a particular mode of viewing things to each eye, but habit combines both the images so received (but which mathematically can never entirely cover one another) into a central one. It is only when both impressions impinge on unaccustomed parts of the retina that they produce different perceptions, in the same manner as we feel a small ball double, if we touch it simultaneously with the external sides of the points of two fingers. We further see with two moving eyes, by which the number of intuitive elements connected with an object are increased. Finally, we are able to move ourselves or the objects, and thus to gain quite different views of one and the same object. Thus we obtain a tolerably broad basis upon which a construction of the figure of objects may be confidently undertaken. Practice in this case makes the master, and we see a great difference between a learned man, who has spent the greatest part of his life in his study, and the sportsman, or still more,

the savage, over whom, from his infancy, the instinctive conceptions of nature have prevailed.

But all these various relations are foreign to the microscope. We invariably, when using it, see with but one eye, generally in a state of rest, and always in a certain given position in relation to the object. We also see the object always in an isolated condition, and cannot therefore form a notion of it by a comparison with impressions from other objects. Further, our eyes possess a certain power of accommodation to different distances, not confined within very narrow limits; we can see objects equally distinct, although they may be at unequal distances from our eye, and we receive our visual impressions in such rapid succession, that it is an easy matter for us to combine all these impressions. This also, for the most part, is wanting in using the microscope, especially with a high magnifying power (and also the more accurately the instrument has been finished), as we only see a mathematical surface. This is particularly the case in the compound microscope, where we do not look at a real object, but merely an image, and there is therefore, for the moment, no other object of sight existing excepting this mathematical surface, and the power of accommodation of our eye is of no use in seeing what may be placed above or below this surface (which is in a manner the profile of the object under examination), but we are compelled to annihilate the one object of sight, and to substitute another in its place. It will easily be conceived how infinitely this must increase the difficulty of combining the separate impressions into one corporeal whole.

Taking the whole of these remarks into consideration, the results will be — firstly, that there is a difference between vision with the naked eye and with the microscope; and, secondly, the fundamental principles from which rules for the conduct of microscopical examination must be sought. In the first place, the instinctive knowledge of the material world is made manifest to us in the perception of form previous to the mathematical conception, for which latter the eye, as the organ of sight, only furnishes us with some few elements, whilst we receive the rest from other senses; the conception derived by the other senses is entirely lost in microscopical objects, and the elements furnished to us by the eye are, moreover, divided during microscopical observation; the separate parts are isolated, and presented to us under circumstances which infinitely increase the difficulty of their combination. Secondly, in order to avoid these disadvantages, and to secure the results of microscopical researches against the errors of judgment arising from the exercise of the faculty of mathematical conception, we must endeavour to increase the number of elements in such a manner as to gain thereby, as much as possible, a perfect and safe foundation for the perception of form.

This task involves the necessity of examining thoroughly every aspect of the same object, and of removing from it everything which does not belong to it. This last part of the task is partially accomplished by improvements in the instrument, in as far as they obviate errors of form and colour (which are based upon the spherical and chromatic aberration). Respecting these two points, which concern the optician more than the observer, we have already before mentioned every thing necessary, and the only concern of the observer ought to be to procure himself the best possible instrument. Besides these, however, there are many other optical phenomena, of which the observer should be conscious, which, although belonging to the image, yet do not belong to the object observed, and with which every one ought to be acquainted, in order to be able to eradicate their share in forming our conception of the nature of the object. To such belong many of the phenomena of colour which are not produced by chromatic aberration. The bending of the rays of light not unfrequently occurs in using the microscope. On observing, for instance, very small holes, perhaps pores of the cellular walls, if the object does not happen to lie exactly at the right distance from the object-glass, the internal surface will appear coloured, and, according to the size of the pore, or the distance from the focus, yellowish, reddish, or greenish. During the observation of very small globules, or other solid substances, a delicate coloured border will be seen under similar circumstances. But both phenomena disappear if the object is brought exactly within the right focal distance. We should therefore always endeavour to get rid

of such colours by placing the object exhibiting them, even when it does so, in the centre of the field, where naturally perfect achromatism takes place in all positions, and should attribute such colours to the object itself, after it has been found impossible to get rid of them by every precaution. The assertion of some observers, that the inner circle of the pores in the cells of the *Coniferæ* (the real pores) occasionally appears to be of a green colour, furnishes an illustration of this kind of error.

Under this head, also, belong certain aberrations of form, which are caused by a defective method of placing the object within the correct focal distance : thus, lines will appear double, or of a certain breadth, which, on being accurately placed, present simple lines, or as sharp lines without any apparent breadth. This is probably a phenomenon of diffraction. In this instance, neither the apparent breadth nor the reduplication of the lines belong to the object itself, as these phenomena disappear when perfect distinctness of the image is obtained by means of a correct way of placing the object. An instance of optical illusion may be found in Mirbel's treatise, "Nouvelles Notes sur le Cambium" (Archives du Muséum d'Hist. Nat., 1839. p. 303. et seq.). He there makes mention of cells (pp. 306, 238, Table xxi. fig. 3. and fig. 6.), the walls of which appeared to be marked on a transverse section by transverse striæ, which, however, disappeared on the examination of a longitudinal section, then presenting longitudinal striæ. I have frequently observed this phenomenon, and have no doubt of its being an optical illusion. Mirbel has been rather too free with his striæ in the plates mentioned, as we never see more (less) than four, viz. the upper and lower cut surface of the cell and two lines. The proof of its being an optical illusion is made evident by the fact, that we can never obtain a sight of two of these lines alone by any change of the focus. They either all four appear, or only the upper, or only the lower surface. I do not find that any one has as yet directed attention to this phenomenon, and much less has any explanation been given of it. It is unquestionably certain that the object only lies in the correct focal distance when its image appears to be most distinctly and accurately represented. But the differences in distinctness and accuracy are so fine, that they frequently hardly become perceptible to the most practised eye. The rule may, therefore, be better given by saying that the correct focal distance has been found when the image appears smallest, and when the dimensions of all the parts, and of all the lines and points of which it is composed, exhibit the smallest size. It will always be found that the greatest accuracy and distinctness exist in that case, where each line and each point appear the darker, the smaller and the narrower they are. There are probably many other conditions which embarrass our judgment with regard to microscopical objects, but at present none else have come within my own cognisance. We find, alas! no information at all respecting these things in the writings of natural philosophers, because no one has as yet occupied himself with the theory of microscopical observation.

Another preparation, besides the knowledge of the optical facts, is necessary for the task of enabling us to distinguish the phenomena that do not in reality belong to the object under observation. These optical facts belong to the image which the object-glass produces, and only occur in the compound microscope. But there are a great number of phenomena which are connected with the real object on the stage, but yet do not belong to the real object of our observation. These likewise interfere during the use of the simple microscope. We must be thoroughly acquainted with these phenomena before we can proceed with any microscopical examination with any hope of success. The requirement, indeed, in this case would be to make ourselves masters from personal observations of all objects already examined, before we proceed to the examination of a new object. But a cursory glance at the results already attained by the microscope shows the impossibility of satisfying such a demand. We must therefore limit ourselves, and instead of so comprehensive a demand, we will state two more practicable, but quite indispensable requirements. The first consists in the necessity of making ourselves acquainted with the general phenomena that may possibly occur on every examination, before we avail ourselves at all of the microscope for our researches ; and the second consists in the necessity of studying accurately, previously, every thing that is already known respecting the special object of our examination. We

can only direct attention to this in the shape of examples. The objects of microscopical examination are either forms or processes.

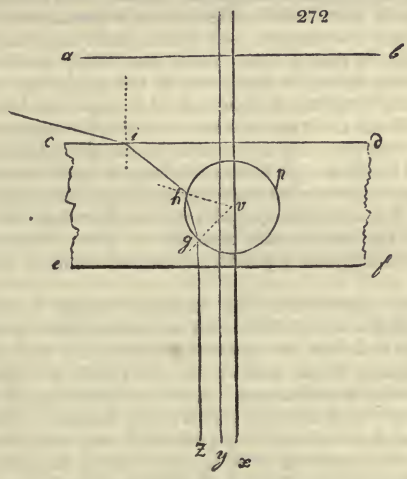
*A.* With regard to the former, we have to consider two kinds of things:

*a.* Actual forms, which are so universally distributed that they may interfere with every examination and obscure its results.

To these belong every thing which in ordinary life we call *dust;* hence small fibres of vegetable or animal tissue, or small granules of inorganic substances.

As most objects, at least all transparent ones, are moistened with water, there belongs to this category the infusoria usually occurring in water, which, without very tedious preparation, by means of boiling and hermetically sealing the water, can never be wholly excluded. These objects should be well known and frequently observed under various magnifying powers and circumstances, so that, being perfectly conversant with them, we may at once exclude them from our consideration as not belonging to the object of our observation, should they be present with it.

*b.* Apparent substantial forms, consisting of substances which are formless. To




such belong all kinds of gas which may be mechanically separated in fluids; also mechanical mixtures of two fluids that do not mix with each other; for instance, bubbles of atmospheric air in water and oil, or drops of oil in water or gum. Air-bubbles especially have caused many microscopical errors, even up to the present day. They always appear under the microscope, when in a fluid, as spherical bodies, with a very black margin and a very small, clear, round centre. On a more accurate examination of them, we may recognise reflected images of objects which happen to be in the vicinity, on the black margin of the side which is turned towards the light, as, for instance, the cross bars of a window-casement, &c. The explanation of this phenomenon is easy. Rays falling parallel from below experience (with the

[272] *a b* Is the object-glass of the microscope; *c, d, e, f,* a layer of water, in which is enclosed *g, h, p,* an air-bubble. The ray of light (*x*) consequently passes directly through the perpendicular axis of the air-bubble; near to it, also, the next rays, as, for instance, *y*. The more remote ones (*z*), on the other hand, impinge obliquely on the tangential plane of *g*, are thus refracted, and that from the perpendicular, from *v—g*, as they pass from a denser into a thinner medium, from water into air; they therefore travel the road *g—h*. They are again refracted at *h*, but of course upwards from *v—h*; they then travel the road *h—i*, and here they once more take a diverging direction, so that none of the rays, which do not pass through the axis of the air-bubble, or close to it, can ever reach the object-glass, and consequently the eye. An air-bubble must therefore appear to be furnished with a broad black lightless margin, and with a bright nucleus. This explanation may be readily applied to other cases of enclosed air.

exception of the central rays) a refraction during their transit from the denser medium into the air, and this diverts them considerably from the rays of the axis; they strike, therefore, the periphery of the atmospheric globule, and on emerging from it again experience a refraction, by which they diverge so far from the rays of the axis, that they cannot arrive at the object-glass, and, consequently, not at the eye. A similar process takes place with all gases enclosed in a fluid. This, even at the present day, is a stumbling-block. We meet with elaborate explanations of a dark material said to be deposited in the membranous glands, and also with theories based upon the observation of them; but, on strict examination, we find that it is only the air enclosed in the stomates which has deluded the observer. Now we have plenty of means of convincing ourselves whether we have air before us or not; for instance, water, which soon imbibes the air, caustic potash, alcohol, oil of turpentine, &c.; but we ought to expect from a practised observer that he should be able to distinguish air from a solid substance by merely looking at it. Air contained in the intercellular passages has also been described as a dark juice. On the other hand, air has been sought for where it can never be found. In many works it is still stated that "the epidermal cells contain air." It only requires a glance through the microscope, and some elementary knowledge of optical science, to convince us that nothing more than fluid, which has nearly equally refractive power with water, is contained in the epidermal cells of any healthy living plant. But such matters are committed to paper, and copied again, without any one inquiring about their correctness or asking for reasons.

Drops of oil present the same appearance under the microscope, only with this difference, that the black margin in the oil-drops is much narrower, owing to the difference of refractive power between air and water being greater than between oil and water, and a greater number of rays are therefore lost in the air-bubble. The explanation is the same in this case as was given when speaking of the air, only the rays take exactly the opposite directions, owing to the greater refractive power of the oil.

Other thick fluid substances, for instance mucus (protoplasma), assume different forms in fluids with which they are mixed, and in which they are not dissolved, and which forms are generally caused by their adhesion to other objects, as, for instance, to the surface on which they are examined, and in that case they are fibrous or membranous; if, on the other hand, they are more isolated, and left to their own cohesive power, they assume a spherical form.

*B.* There are also processes very generally met with which a microscopic observer ought to be acquainted with, in order not to be deceived by them when they occur. Certain motions, first of all, belong to such.

*a.* Robert Brown, the gifted English botanist, first made the important discovery, that all substances, organic as well as inorganic, on being suspended in a fluid in sufficiently small particles, are in a state of constant trembling or vibratory motion, similar to a mass of monades, when seen with a low magnifying power. The motion is difficult to be characterised, and it can only be accurately comprehended, and distinguished from other similar motions, by frequent observation. It has been frequently observed in parts of plants, for instance, in the fine granular contents of the pollen-cells, and has been described as a special living action, which it certainly is not. We know nothing yet of the origin of these movements; but they are probably owing to slight electrical tensions and compensations.

*b.* Another movement, which is frequently seen, is produced when two different fluids, which have a considerable affinity for each other, for instance, water and alcohol, or water and solution of iodine, are mixed with one another. A powerful current usually takes place in them, frequently in quite opposite directions.

*c.* A third case is, when fluids rapidly evaporate. During this process there usually takes place a double current, namely, an upper one, from the margin to the centre of the drop, and a lower one, from the centre towards the margin.

*d.* There are two further occurrences to be observed, which give rise to frequent illusions; one of them is the process of solution. Since most objects are in a fluid, when under observation it frequently happens that a solution of many objects takes place. The movements and changes of form occasioned thereby

ought to be recognised. The other is the process of coagulation, which is also produced by the influence of the surrounding fluid upon the substances under observation. In this respect great caution ought to be used in the examination of organic bodies, since apparent formations are frequently produced by such coagulatlon, with which the nature of the thing has nothing to do. The best rule in this case is always to examine organic objects in as fresh a state as possible, and to prefer unconditionally the image which exhibits itself at first sight, to all others, and to regard it as normal, when a frequent repetition of the observation has convinced us that we have taken a correct view of it at the first sight. Meyen has frequently described and represented coagulations of mucus and other substances as forms (cells), for instance, in his Physiologie, III., Plate X., fig. 6. Mirbel has done the same in his work, Sur le Cambium, &c., Plate XX., fig. 2. Finally, we must direct particular attention to the second point above mentioned, and which must be substituted for the exorbitant general requirement, viz., that the microscopical observer should, before he proceeds to any research, make himself most intimately acquainted with every thing that has already been observed and made known with regard to the respective objects of his research.

We now proceed (to make use of a medical expression) to the second indication, namely, to the many-sided comprehension of one and the same object. To do this in the preparation of an object for microscopical examination, we must consider how we may obtain from such object, properly prepared, as many views as can possibly be obtained from it, in order to construct a clear image from the combination of the individual conceptions. In this respect there is least difficulty in the observation of opaque objects, since the object is here brought in any manner we please into the focus of the object-glass, or of the simple lens. It is simply laid in a suitable position on a small glass plate, and the latter on the stage of the microscope; or it is taken up between the small forceps, which are usually given with every microscope, by which we obtain the advantage of turning it round under the microscope, thus enabling us to view it on all sides.

The observation of transparent objects is attended with much greater difficulty, and, in fact, they form generally the objects of more accurate scientific examinations. The object, in itself, is seldom so transparent as to enable us to bring it under the microscope in an unprepared state. The wetting with water or with other liquids, as fixed or volatile oils, Canadian balsam, &c., is of great assistance. Generally we are compelled to make fine sections of the object, which, when sufficiently thin, are always transparent, as, amongst organic substances, which form the most important objects, we have no perfectly opaque objects. A double knife has been invented for making such sections, which, however, is only calculated for a very few botanical objects, its performance being anything but perfect. (Valentin, Répert. vol. iv.). There is in fact no alternative but that of obtaining the necessary skill by practice, so as to enable us to cut very fine slices by hand. The anatomical scalpel was in former times commonly made use of for this purpose. Subsequently very thin two-edged knives, in the shape of the grafting-knife, were recommended, instead of the scalpel. I have found that a good razor with a sufficiently heavy blade is the best instrument; it may either be used merely with one's hand, or by putting the object between one's thumb and fore-finger, and then cutting through it. In this manner an accurate section may easily be obtained of small objects, which may again be taken in the same way between the fingers, and a thin slice cut off as before. If the object happens to be very delicate and thin, as, for instance, hairs, the leaves of moss, &c., it must be attached to the nail of the thumb, by means of a little oil or saliva; the edge of the razor is then placed upon it diagonally, and a to and fro motion is made with it, gently advancing towards the root of the thumb. In this manner we may readily obtain a number of thin segments, of which some are always perfectly available. One great difficulty which we have to get over in this process consists in the great softness of the object, which opposes so little resistance to a knife, that even the sharpest blade tears and crushes rather than cuts it. I have invented a method, which I have often applied with great success, in order to remove this evil, and several of my friends have also availed themselves of it in the observation of animal substances. We first prepare, namely, a very concentrated solution of pure colourless gum arabic, and soften the object to be investigated

thoroughly in this mucilage. It can then be readily fixed to a small board, on which it must be perfectly dried, whilst a small quantity of the mucilage is occasionally poured upon it. Before, however, it has become so dry as to cause the gum to resume its brittleness, delicate sections of the object are made, which are then wetted with a little water on a small glass plate; the gum imbibes the water, and the object assumes again almost its pristine form.

Such a preparation with the hand, however, does not suffice for very accurate investigations. Indeed, the view of a section is by no means of importance in many objects; and the thing to be desired is a division of the object into the separate parts of which it is composed: and here we must have recourse to the microscope in order to prepare the object properly. The simple microscope is the most suitable for this purpose, which, especially when Chevalier's or Wollaston's double lenses are employed, still affords sufficient space between the object and the lens, at a magnifying power of 100 times, to enable us to work with very delicate instruments. The compound microscope has the great disadvantage, that the object is reversed, requiring, therefore, a very difficult practice of opposing the motion; and in the next place, our hands are so far removed from the eye as to render their movements uncertain, so that a tearing or crushing of the object at random is scarcely avoidable.* But the greatest hindrances to preparing under the microscope are the instruments. They are, of course, magnified as much as the object; and we soon find that no point is sufficiently fine to enable us to divide the parts of the object with accuracy: very fine needles, which we may sharpen ourselves upon a very fine grindstone, afterwards observing the edge and point under the microscope, are the best for this purpose. English needles, intended for very fine operations, and sharpened in the same way, will answer the purpose. The other difficulty is less easily overcome, viz. the circumstance that our hand is not used to such delicate movements as are necessary at a magnifying power of 50 or 60: practice, however, will serve to remove this impediment.

After these preliminary considerations, I shall now proceed to the methods by which the object under investigation may be placed in as many different circumstances as possible, in order thereby to increase the number of points of view. Optical, mechanical, chemical, and physical auxiliaries are here to be distinguished. They may be called, generally, microscopical reagents.

### a. *The Optical.*

First of all, we may remark, that the observer should never limit himself to the observation of an object by one magnifying power alone. It is always advisable to commence with the lower powers, and gradually to use the higher ones. This mode of proceeding is necessary on account of the fact that the field of vision must diminish in proportion to the degree of magnifying power; and as it is always requisite, in order to obtain a correct conception, to have a distinct view of the individual parts in all their relations.

2dly. The changing the direction of the light is also a matter of importance, as we have already explained.

3dly. It is frequently of advantage to observe an object in a coloured, or, still better, in a monochromatic light: this may be done by using coloured glass for the stage, or employing a spirit-lamp for the illumination, the wick of which has been previously dipped in a solution of common salt, or in which the spirit has been previously diluted with water as much as possible. Both methods, according to Brewster, give a homogeneous yellow light.

Finally. It is advisable in many cases to observe the object by polarised light, for which purpose a crystalline body, suitably polished for it, is fastened under the table of the microscope. But any working-optician will supply information on this subject: I need not, therefore, make any further remarks upon it.†

* An erecting eye-piece in the body of the compound microscope obviates nearly all objections to it as an instrument for dissection.—Trans.

† Compare Chevalier, Des Microsc. et de leur Usage, pp. 125—128. [For further information on this subject, the English reader is referred to a little work, by Mr. C.

b. *Mechanical Means.*

It is advantageous in many respects to observe how an object alters on the application of pressure. A double disc was formerly made use of for this purpose: this, however, was attended with the disadvantage that we could only observe the result, not the gradual effect, of the pressure. More recently, an instrument invented by Purkinje, and which bears the discoverer's name, has been made use of for this purpose, and also an improved form by Shiek. The gradual effect of the pressure can very readily be observed under the microscope with this auxiliary. The value of this instrument has been overrated by Purkinje, but has been very unjustly rejected altogether by Meyen. It is, perhaps, the only means of distinguishing a small globule from a vesicle, which latter, without having any real existence, occupied so prominent a position for a long time in botanical works.

c. *Chemical.*

The different phenomena which a substance presents upon the application of chemical reagents are of the highest importance for the formation of our opinion. Indeed, it very frequently occurs that we are obliged to determine substances according to their chemical nature, which, enclosed in organised bodies in a small quantity, cannot mechanically be separated from them, at least not in such a manner as to enable us to institute a chemical analysis of them. There is no other means left to us, therefore, but to use such agents under the microscope itself.* The principal of such reagents are: —

1. Tincture of Iodine. Particularly useful for rendering visible very transparent objects, and for the determination of various vegetable substances.
2. Sulphuric Acid. For the destruction of certain parts.
3. Fixed Oils. The best of all is the oil of almonds. Volatile oils, oil of lavender, alcohol and ether, and Canadian balsam, in order to render objects transparent, and to dissolve species of fat and resin, and bring substances into a state of coagulation; as, for instance, albumen.
4. Solutions of Sugar, Gum, and Albumen. In order to prevent endosmosis, and the changes of form consequent thereon.
5. Solution of Caustic Potash. For the destruction of certain parts.
6. Acetic Acid, Nitric Acid, Muriatic Acid. In order to dissolve many substances.

The reagents enumerated last (under No. 6.) ought to be avoided as much as possible, when the achromatic microscope is made use of; and at all events the object ought to be covered by a glass plate, since the evapórating acids very readily produce an effect upon the very susceptible flint-glass.

d. *Physical.*

It may occasionally happen to be of interest to observe the effect of heat and electricity upon certain objects under the microscope. Peculiar contrivances are necessary for this. The application of heat requires glass plates that have previously been thoroughly annealed, which may be heated by means of a small spirit-lamp at one end, or by means of very thin glass plates loosely put into a brass frame, and heating the latter. For the observation of electrical effects we have a small peculiar stage, on both sides of which two small forceps hold moveable little pieces of a glass tube, through which wires are drawn. These wires reach the stage at one end, and have a small hook at the other, in order to attach the conducting wires.

Many errors, which but too frequently occur in botanical works, will be avoided if the auxiliary means enumerated above are applied, and if attention is paid to the cautions and hints communicated. Once for all, however, I must repeat the fundamental rule, that he who wishes to observe with success, must observe frequently and with the most profound attention: by observing this rule, he may gradually learn to see, for *seeing* is a very difficult art.

Woodward, on polarised light; and also the Transactions of the Microscopical Society. — TRANSLATOR.]

* J. Vogel, Anleitung zum Gebrauch des Mikroskops, &c.

# EXPLANATIONS OF THE PLATES.

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## Plate I.

Figs. 1—16: see § 14.

*Fig.* 1. Contents of the embryo-sac of *Vicia faba* soon after fecundation. In the clear fluid, which consists of gum and sugar, swim granules of protein compounds (*a*), amongst which are some of a larger size. Around these last the first are rolled together so as to form a little disc, and sometimes two such discs are seen blending one with the other (*b*). Around other discs can be discerned a clear, sharply-defined edge (*c*), which gradually extends further from the disc (the cytoblast), and at last may be clearly distinguished as a young cell.

*Fig.* 2. Young and very irregular cells from the albumen of *Vicia faba*, with beautiful parietal cytoblasts and nuclei.

*Fig.* 3. Free cytoblasts in the sac of the embryo of *Sanguinaria canadensis;* three of them are hollow (?), with a firm nucleus.

*Fig.* 4. Cytoblasts with nuclei from the embryo-sac of *Pimelea drupacea:* *a*, Free cytoblast with nucleus; *b*, a cytoblast with two nuclei; *c*, cytoblast with three nuclei, and the cell forming around it.

*Fig.* 5. Cytoblasts from the sac of the embryo of *Fritillaria imperialis*, in various stages of development.

*Fig.* 6. Some cells from the albumen of the same plant, having a correct relative size to the foregoing figure. The cytoblasts are partly round (*a*) and partly lenticular (*b*); they are always, through a peculiar substance, firmly adherent to the wall.

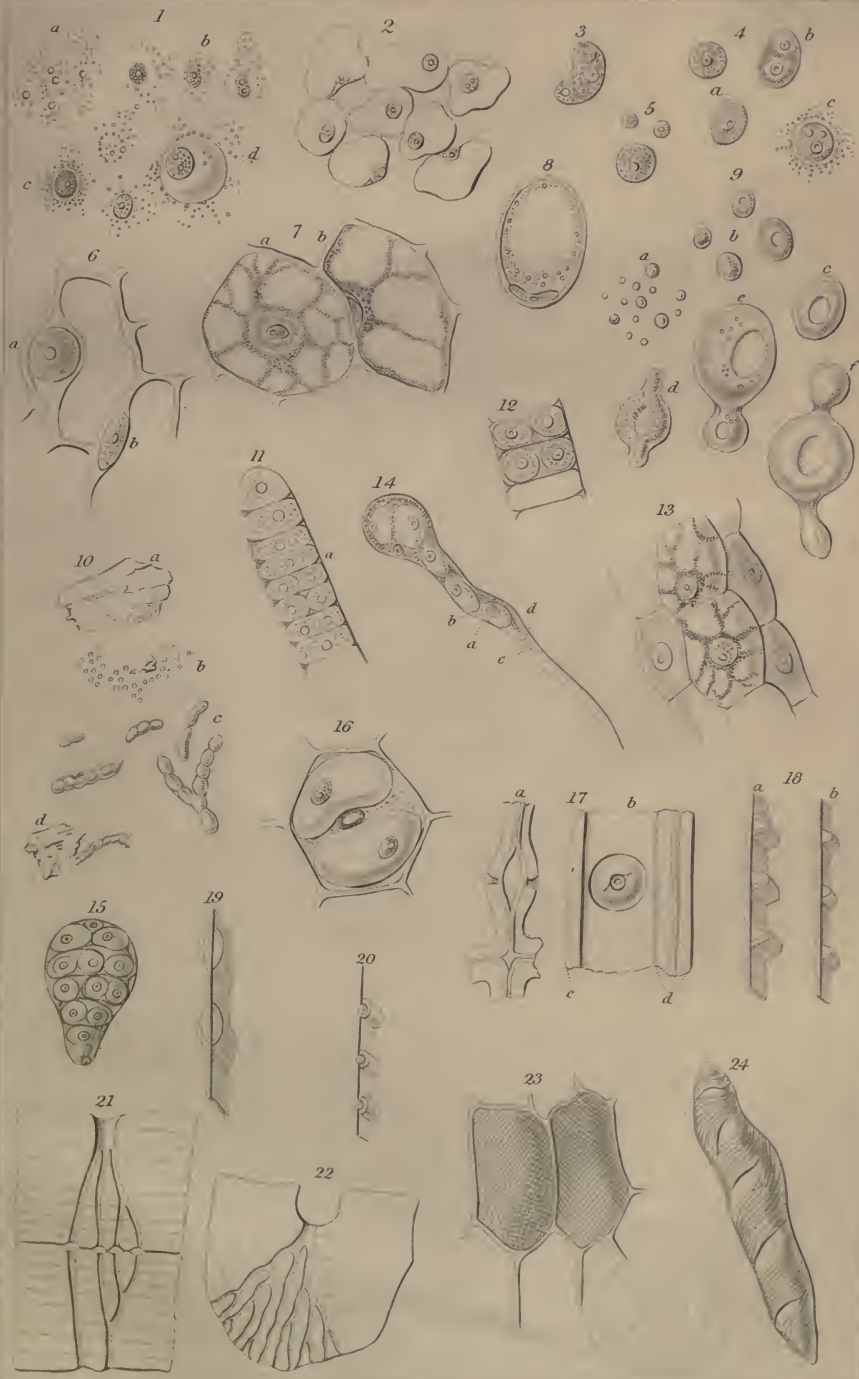
*Fig.* 7. Cells from the albumen of *Pedicularis palustris*. *a*, The single wall of the cell; *b*, section of the surface of the cell in focus. Around the cytoblast is seen a great quantity of a muco-granular substance, which moves in little reticular streams on the inner surface of the wall.

*Fig.* 8. Mature pollen-grain of *Fritillaria imperialis*, with parietal cytoblasts; the great central cavity is the result of endosmosis.

*Fig.* 9. Formation of the fermentation-fungus in currant-juice (page 37.). *a*. The first appearance of solid matter (protein?) in the clear juice. These globules pass gradually into the forms at *b*. These are found suspended in the juice when it begins to become opalescent, and before the slightest trace of the development of gas or of fermentation can be detected; *b* and *c* are transitionary stages; *d*, *e*, *f*, ferment-cells in various stages of increase.

*Fig.* 10. Decomposition of pure protein in a solution of sugar (during fermentation), page 37. *a*. A small portion of protein breaking up into granules (*b*) at the under part; *d*, a portion of protein, with the edges well defined on one side, and at the other breaking up into little granules, from which proceeds, indistinctly at its commencement, a little cellular fibre; *c*, various forms of cellular fibres produced in the fermentation of a solution of sugar with pure protein and protein compounds.

*Figs.* 11—13. Gradual development of the hairs on the stem and leaves of *Glaucium luteum*. In the original elongated epidermal cells, transverse cells are formed, which are clearly seen to be free. At *a*, one of these cells displays two

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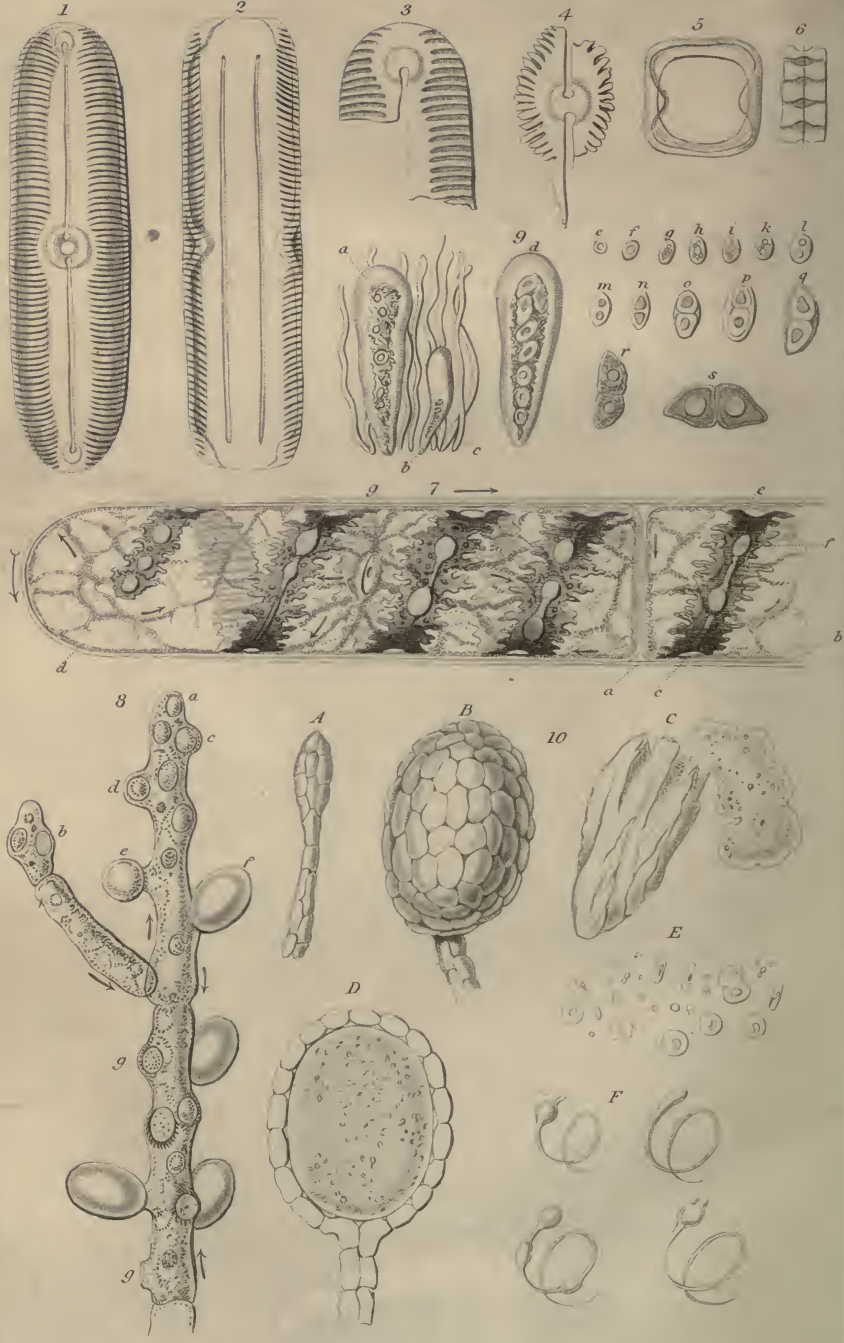
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others in its interior; under this is a second of the same kind, and below this is a third containing two free cytoblasts.

*Fig.* 12. A condition somewhat later than fig. 11. *a.* The encasing of the cells in one another is very evident.

*Fig.* 13. A part of the living hair. Reticulated streamlets proceed from the cytoblast in all the cells, but they are drawn in only two of the cells.

*Fig.* 14. The first commencement of the formation of an embryo in *Pedicularis palustris: a, b.* and *c, d.* display the outline of the embryo-sac in the region of the penetrating pollen-tube, which at the end, in the embryo-sac, is swollen globularly, and contains two very young cells and a free cytoblast; below in the pedicel there are three oval, free cells.

*Fig.* 15. Very early condition of the embryo of *Sagittaria sagittæfolia.* It may be here seen how the pollen-tube, loose at the beginning, is gradually formed into a little cellular body by the continued formation of cells in cells.

*Fig.*16. First commencement of an oil-duct in the tubers of *Georgina variabilis.* In a single cell of the parenchyma, two free cells have been formed, which have already separated between them a large drop of oil, and are characterised by their cytoblasts.

Figs. 17—24: see § 18—19.

*Fig.* 17. Porous cell-walls in *Abies excelsa: a.* transverse section. The two primary cell-walls are clearly separated (Hartig's *Eustathe*), and the deposit-layers are penetrated by the pore-canals (Hartig's *Astathe* and *Ptychode*). *b.* The longitudinal section: it displays at *c.* the simple wall of the cell, at *d.* the double wall of this and the neighbouring cell.

*Fig.* 18. A delicate section from the wall of the spiral-fibrous cells in the leaf of *Oncidium* (*altissimum?*). The spiral fibres appear separated from the original cell-wall by a sharp line. The bark (external layer) of the fibre is not to be distinguished in the thinner and younger fibres, *b.*

*Fig.* 19. A similar section, as in fig. 18, from the leaf of *Vanda teretifolia*, but upon the double wall there are two spiral fibres lying one on the other. The external layer of the individual fibre is at least as thick as the doubled wall of the two cells.

*Fig.* 20. A similar section of an annular vessel in the stem of *Arundo Donax.* The external layer of the annular fibre is at least three times as thick as the original cell-membrane. The internal portion of the spiral fibre was treated with warm caustic alkali, it swelled up, and became gelatinous without changing the original cell-wall, or the external membrane of the spiral fibre.

*Fig.* 21. In the gynophore of *Magnolia grandiflora*, after flowering, the cells are very thick, and consist of several layers which are traversed by branched pore-canals. The figure displays two of these projecting one against the other. The pore-canals pass through the layers of the cell often at right angles.

*Fig.* 22. The pore-canals as above are seen to represent a very thickened cell from the bark of *Fraxinus excelsior* var. *jaspidea.*

*Fig.* 23. Two cells from the tuber of *Georgina variabilis* with delicate spiral fibres.

*Fig.* 24. A cell from the root membrane of *Oncidium altissimum*, with delicate spiral fibres, which in some places separate from each other. These spaces appear at a later period to produce an actual perforation of the primary cell-wall.

## Plate II.

Figs. 1—6: Siliceous Shield of *Navicula viridis* (§ 82.).

*Fig.* 1. Anterior view. In the middle line are two clefts, each about half the whole length, and terminating at the centre, as well as at the other ends, with a little circular enlargement. This is seen more clearly in figs. 3. and 4. Above, below, and in the middle, upon the anterior and posterior surface of the shield,

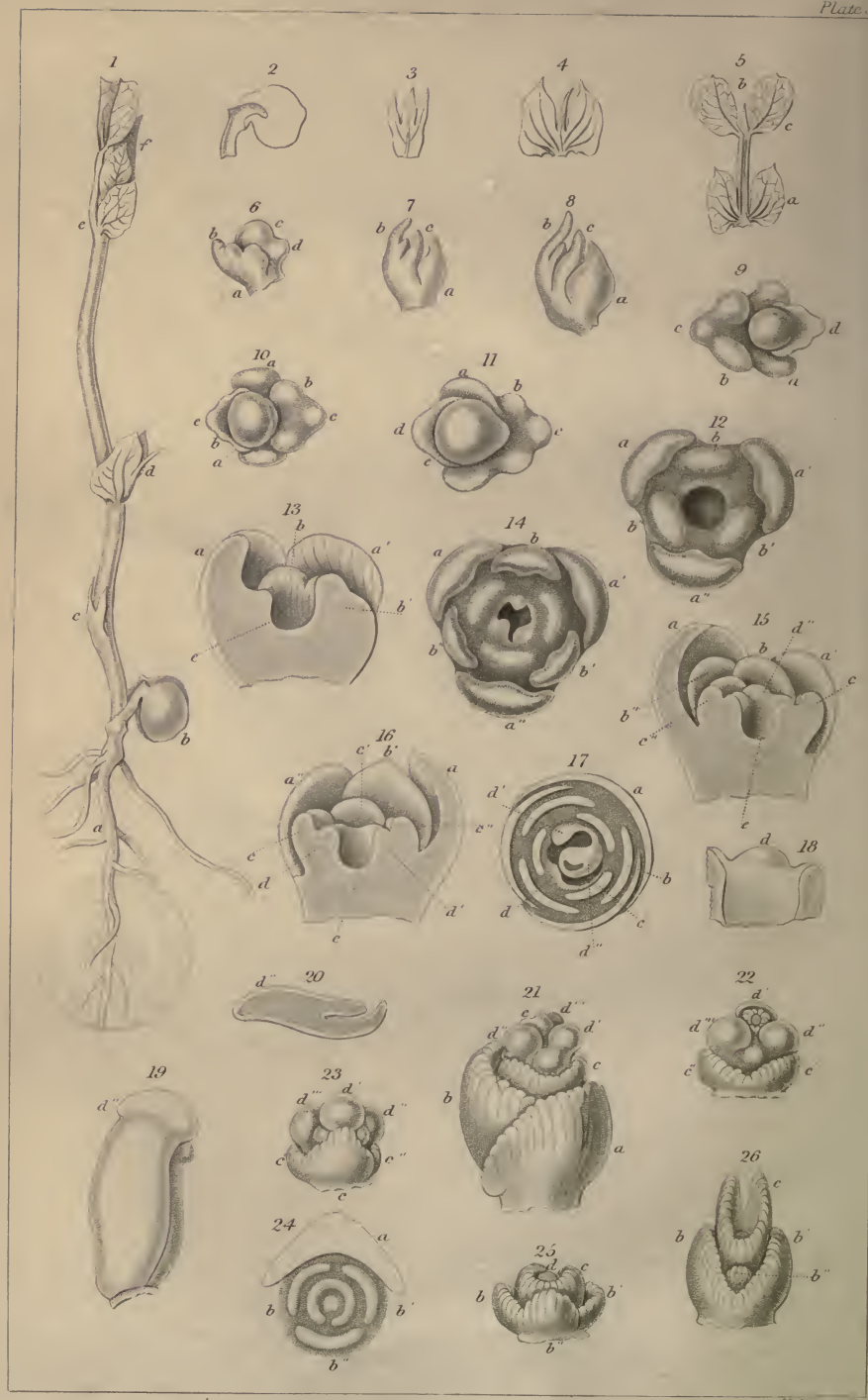
are seen thickened spots of siliceous matter (like drops of glass on the surface of a bottle); but by no means a round hole, as it is represented by Ehrenberg and many others. That such a hole is decidedly sometimes not present in the centre, is seen unanswerably in such fragments as fig. 3., and especially fig. 4., which may be easily obtained by crushing the shield. On each side the central clefts are seen a great number of oblique clefts, which, according to the direction of the light through the focus, appear smaller or larger. In these spots the shield consists of two leaves lying one over the other. These leaves are penetrated with the small clefts which, where both the lamellæ touch each other, are somewhat broader, which explains the varying breadth of the clefts according to the alteration of the foci. Fragments in which this structure is clearly represented may be frequently obtained by crushing the shield (fig. 6.).

*Fig.* 2. Lateral view of the shield. The three enlargements are seen here on both sides, from which it is very evident, and what we might have supposed at first sight, that the central enlargement is a little depression upon the external surface. The two sides of the shield exhibit only a few of the oblique stripes: in the centre is seen a broad smooth surface, which is traversed in its whole length by two parallel clefts. In this figure is seen more strikingly than in fig. 1. the double contour which denotes the thickness of the wall of the shield, and which suddenly ceases both above and below. This clearly shows that a passage exists from the top to the bottom of the shield, which may be easily confirmed, if the shield, or, what is better, the same obliquely fractured, is looked at from above. This may be done by taking some of the siliceous earth of Erbsdorff and mixing it with mucilage, and before it is perfectly hardened cutting off delicate plates with a razor. Fig. 5. exhibits a section of the upper part of a shield prepared in this way.

Such an artificial and complicated structure amongst plants has no explanation, and is entirely without signification. In all actual plants we find the silica present in quite a different form, as little separate scales or drops, and distributed through the substance of the cell-wall.

*Fig.* 7. *Spirogyra quinina* (§ 82.) The end of a filament of the plant. A threefold wall of the cell may be distinguished. Externally, a gelatinous covering (*a*), which extends over all the cells of the fibre; under it lies the special cell-membrane (*b*). Both are transparent, and separated by a delicate black line, and are easily distinguished from one another, especially at the commissures where two cells unite. The cell-membrane is clothed on its inner surface with a delicate but clearly distinguishable pale yellow layer, of a semi-fluid proteinaceous substance (*d*). Upon this layer lie the bands, dentated at their edges, of chlorophyll (*e*), the basis of which is probably wax. These bands are externally furrowed, and take up in the furrows a clear firm substance (*c*), which may be easily distinguished from a mere interspace if the whole fibre be moistened with tincture of iodine. In the continuity of this transparent substance (vegetable jelly) there exist individual larger or smaller granules (*f*), which, at least at certain times, consist of starch. Accidentally in the midst of the cell there exists a somewhat elongated cytoblast (*g*), which contains a nucleolus surrounded by an areola of mucous matter, from which proceed on all sides little streams towards the wall of the cell. There is always in the nitrogenous layer a circulation consisting of innumerable very varying streams which unite together in a reticular manner. The direction of some of these is shown in the plate by the direction of an arrow. These little streams are so changeable, that if a drawing from nature be made of the system of streams, in the course of a quarter of an hour, on comparing it with the original it will be found that every one of the streams has taken a different direction. If a representation of the new streams is made, and thus on from one quarter of an hour to another, it will be found that they keep on changing, and that the whole layer of nitrogenous matter takes part in the movement of the little streams. The remainder of the contents of the cell contains a transparent fluid.

*Fig.* 8. Mould found growing on the stems of *Passiflora alata;* the upper part of the little plant with a lateral branch. In this case also the nitrogenous layer circulates in little streams. This little plant exhibits a tolerably complete history

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of the development of the spore of the fungi, if the steps *a, b, c, d, e, f* are compared, whilst *g, g* represent the cicatrices of pollen-spores : see the text, § 84.

*Fig.* 9. *Borrera ciliaris.* Development of the spore, § 88. *a.* A full-grown spore-case filled with a thickish cytoblastema, in which can be discerned individual cell-nuclei. The wall of the spore-case is gelatinous and very thick ; *b* is a much younger spore-case ; *c*, the fibres of which the disc of the sporocarp is formed (§ 88, fig. 127.) ; *d*, a spore-case with almost perfectly-formed spores. If the spore-cases at the various stages of their growth are separated from the sporocarps, and their contents accurately examined, they will be found to constitute a series such as are represented from *e* (a free cytoblast) to *s* (a perfectly ripe spore). In *f* is seen the formation of the primary simple spore, in *g, h, i* the gradual destruction of the nucleus, in *k, l, m* the appearance of two cytoblasts, around which, from *n—q*, two cells organise, till at last, in *r* and *s*, the primary spore is dissolved, and the double spore appears perfectly completed.

*Fig.* 10. *Sphagnum cymbæfolium* (*A.—E.*) and *Polytrichum commune* (*F.*). Formation of the *Antheridia* (§ 102. *D.*) *A.* Youngest condition of *Antheridia* ever observed by me. *B.* Perfectly-developed organ, consisting of a cellular peduncle and an oval sac, which are formed out of a layer of cells and a large central cell, as is shown in the section, fig. *D.*, which was accidentally made. *C.* The central cell isolated and burst by gentle pressure, with its contents, consisting of gum, sugar (?), albumen, and half-solid, nitrogenous (?) granules. *E.* The contents of the central cell at a later period, consisting of free cytoblasts and very delicate flat cells, in which the nucleus is yet recognised, and which gradually elongates and appears to be converted into the moving spiral fibres. *F.* Various forms of moveable spiral fibres (so-called *spermatozoa*). The so-called head is evidently unessential, as its form is constantly changing.

## Plate III.

### Figs. 1—11. *Pisum sativum.* History of Development of Leaf.

*Fig.* 1. Germinating plant. *a*, Root ; *b*, cotyledons ; *c, d, e, f*, first to fourth leaf.

*Fig.* 2. A cotyledon seen from the inner side. Where the sheathing petiole passes into the disc of the leaf, are seen two little processes, which are the first indications of stipules, and formed by the upward pressure of the bud during its development.

*Fig.* 3. Second leaf seen from the back, small lanceolate, with two lanceolate (so-called adherent) stipules.

*Fig.* 4. Second leaf seen from the back, small lanceolate with two large stipules.

*Fig.* 5. Third leaf, front view, with two leaflets and two stipules.

*Fig.* 6. Terminal bud. *a*, Leaf spread out ; *b*, point of the same ; *c*, termination of the axis ; *d*, plane on which the leaf originates.

*Fig.* 7. Third leaf separated from the foregoing terminal bud. *a.* Stipules ; *b*, point of the leaf ; *c*, leaflets.

*Fig.* 8. Fourth leaf of the same bud. *a, b, c.* The same as in the last figure.

*Figs.* 9—11. Three terminal buds in various ages of the leaves, seen from above. The leaves of figs. 11 *d*, 10 *c*, 9 *d*, 10 *c*, 11 *c*, 9 *c*, exhibit a perfect series of stages of development, which may include also those opposite figs. at 10 *e*. and 11 *d*. at the youngest period of growth. It results from this, with direct evidence, that the stipules are the last parts of the leaf to appear, as they originate in a part of the stem where no other parts of the leaf are ever found. It is also impossible that the stipules should alternate at any time with the first pair of leaflets.

### Figs. 12—20. *Canna exigua.* Development of the Flower.

*Fig.* 12. Youngest condition. The calyx (*a, a′, a″*) and the external circle of the corolla (*b, b′, b″*) are as yet alone present, but long before this the cavity of

the germen is formed through the cup-shaped, spreading flower-stalk, which is easily understood through a longitudinal section of the flower, as seen in fig. 13, where *e* represents the cavity of the germen.

*Fig.* 14. A somewhat later condition. The inner circle of the corolla has appeared. Alternating with these and the most external circle we have three little elevations, forming a fourth leaf-circle of the flower.

*Figs.* 15, 16. Perpendicular sections of the last, in which the four circles of leaves are figured *a*, *b*, *c*, *d* from without inwards. This section does not exhibit accurately the centre of the corolla.

*Fig.* 17. The same in much later circumstances (the whole flower was three-quarters of an inch long), seen from above. The parts of the flower have been cut away about half a line above the germen: *d′* is the leaf of the innermost circle, which becomes the stamen; *d″* is the leaf of the same circle, which is folded together to form the style, and is already grown together by the edges; *d* is the third leaf of this circle, which is aborted.

*Fig.* 18 represents a longitudinal section of the leaf (17 *d.*) seen from within.

*Fig.* 19. A somewhat earlier condition of the style, before the edges of the leaf are grown together, as is more clearly seen in the transverse section, fig. 20.

Figs. 21—23. *Agrostis alba* Schrad. Development of the Flower.

*Fig.* 21. A very young ear: *a*, *b*, the two bracts (*calyx* Linn., *glumæ* Auct.); *c*. the flower-envelope (*corolla* Linn., *paleæ* Auct.); *d*, anthers; *e*, germen.

*Figs.* 22, 23. Flowers from the same ear, seen from two sides. The letters signify the same in both figures: *c c′ c″*, three perfectly separate leaves of the flower-envelope standing upon the same level; *c″* is already somewhat larger than the other two (*palea inferior*), *c* and *c′* grow together at a later period (*palea binervis l. superior*): *d′ d″ d‴* the stamens. Between *d‴* and *d″* (fig. 22). is seen a little wart, and at *d′* (fig. 23.) are seen two: the three stand upon the same plane, and, like the large warts (leaves), form a nectary (*squamulæ* Auct.), which are not seen in the further development of the flower. The three stamens (fig. 22.) enclose the germen from which the nucleus of the seed-bud projects.

Figs. 24—26. *Carex lagopodioides.* Development of the female Flower.

*Fig.* 24. Very young condition of the female flower, seen from above: *a*, bract cut through; *b b′ b″* the three at present perfectly free leaves of the flower-envelopes, of which *b* and *b′* grow together with one another, and form the flask-shaped tube, which latter surrounds the germen, whilst the third leaf is not developed. This flower-envelope encloses a carpellary leaf not yet closed, and the nucleus of the seed-bud.

*Fig.* 25. The same flower seen from the side: *c*, carpellary leaf; *d*, nucleus of the seed-bud; *b b′ b″*, as in fig. 24.

*Fig.* 26. A flower in a somewhat later condition. The two leaves of the flower-envelope *b* and *b′* are now grown together, and surround the third, *b″*, which retires in its growth, and at last entirely vanishes. *c*. The developing germen.

## Plate IV.

Development of the Parts of the Flower of *Passiflora*. Figs 1—4. are *P. princeps*. The remainder *P. cæruleoracemosa*.

Figs. 1—11. Development of the Parts of the Flower generally.

*Fig.* 1. A very early condition of the flower (about one-fourth of a millimeter in length). Around the elevation of the pith in the centre (the termination of the stem) are five foliar organs (calycine leaves, sepals), already become slightly irregular in their development, and in the early condition of the *foliatio valvata* (§ 134.).

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*Fig.* 2. Longitudinal section of the same. The letters indicate the same sepals. An epithelium distinct from the parenchyma can be clearly seen.

*Fig.* 3. A later condition. The sepals have already the commencement of the wing-shaped keel upon their backs. The foundations of the bud are perfectly developed.

*Fig.* 4. Longitudinal section of the same. The same letters designate the same sepals. Between the two there is a leaf of the corolla, and in front of *b* another cut through. Right and left of the corolla-leaf, in the middle, are two little elevations, which are the commencement of stamens cut through.

*Fig.* 5. A somewhat late condition (the bud with the bracteola, about $1\frac{1}{2}$ millimeter long): the three calyx-leaves (sepals) alternate with the two corolla-leaves (petals), and between these there is a little elevation, which is the first appearance of a stamen-leaf (stamen). The two last figures are somewhat smaller than half, so that the wart-like termination of the axis in the centre is not seen.

*Fig.* 6. A later condition. The five sepals are distinct. The petals are seen alternating with them, and the stamen with these. In the centre the axis is conspicuous as the germen (*cauligenum*) with a cavity, but as yet no trace of a style (carpellary leaf).

*Fig.* 7. Longitudinal section, later still. The whole flower is perfectly developed. *a*, Longitudinal section of sepal; *a′*, a second, seen from the edge; *b*, petal; *a* and *b* are attached to a cyathiform extension of the axis *f*, (a disc); *c*, section of stamens; *d*, another from the side; *e*, pistil.

*Fig.* 8. The pistil at the same stage of development, seen from above. Three carpellary leaves are seen at the edges of the germen.

*Fig.* 9. Outline of a transverse section of a corolla, directly above the pistil. The petals still exhibit the valvate condition of the bud. In the three last tissues, where all the leaf-organs are formed, from the calyx to the carpellary leaves, there is not the slightest trace upon the disc of the presence of the *corona*. It cannot, therefore, be formed from the foliar organs.

*Fig.* 10. A longitudinal section in a yet later condition. *a*, Sepal; *b′*, petal seen from the edge; *c*, stamen cut through; *c′*, lower part of the germen and disc *f*, upon which, at *g*, the various forms of the corona begin to be developed as mere cellular (hair-like) growths.

*Fig.* 11. An almost complete longitudinal section of the entire flower, at a yet later period. *a*, Sepal (lower half) cut through near the wing-shaped keel; *a′* sepal seen from the edge; *b*, petal; *b′*, another seen from the edge; *c*, lateral view of a stamen; *c′*, lower part of a stamen cut through; *d*, germen (*germen cauligenum*) cut through: on both sides the commencement of the seed-bulbs project into the cavity; *e*, style (carpellary leaf), with a lateral view of the stigma; *e′* another, with the canal exposed; *f*, enlargement of the axis between the calyx and petals (disc); *g*, continuation of the axis above the petals (filaments); *h*, continuation of the stamens (gynophore); *i*, corona.

Figs. 12—18. Development of the Anthers.

*Fig.* 12. Transverse section of anthers of fig. 7.: *a*, groups of strongly thickened cells; *b*, foundation of vascular bundles; *c*, foundation of four anther-valves.

*Fig.* 13. Transverse section of part of an anther-cell, at a period between figs. 7. and 10. *a*. Epithelium. *b*. Developing cellular tissue with great cytoblasts, out of which at a later period the various layers of anther-valves are developed. *c*. Primitive parent-cells, with great parietal cytoblast for the formation of pollen. After these cells are perfectly formed and arranged by the formation of cell within cell, there originates in every cell an individual cell which is perfectly and easily separable, and these remain isolated when the first are dissolved up. In the isolated cells (parent-cells of Nägeli; they might be called special parent-cells) are formed four free cytoblasts, and around these are formed four free cells.

*Fig.* 14 exhibits the last condition. *A*. A parent-cell in which are two active (pollen) cells and a cytoblast: the fourth lies on the other side, and is not seen. *B*. An individual pollen-cell separated from another parent-cell of the

same kind: it exhibits a large cytoblast and a very evident circulation in streamlets. The pollen-cells are empty, but the parent-cells are full of a thickened muco-granular (especially nitrogenised) contents. Gradually the contents of the parent-cell become clear and gelatinous, whilst the four pollen-cells get filled with a similar substance to that contained earlier in the parent-cells. This is seen in

*Fig.* 15. Parent-cells at a period the same as fig. 11. The parent-cells soon become dissolved, the pollen grains begin to assume a round form, and to separate the external pollen membrane. During this time the cellular tissue of the anther-wall (fig. 13. *b.*) becomes developed and arranged.

*Fig* 16. A somewhat later condition than fig. 11. The pollen grains are quite completed (as fig. 17.) *a*, The perfectly developed epidermis; *b*, the cell-layer, in which is evident a circulation in reticulated streamlets (later spiral layers); *c*, somewhat elongated cells, containing chlorophyll grains; *d*, cells still more elongated, very flat, and containing opaque (nitrogenous) contents; *e*, radical, elongated, sac-formed cells, in which a process of cell-formation is going on, and which contain two free cells with large cytoblasts; these cells are subsequently entirely resorbed.

*Fig.* 17. A perfectly-formed pollen grain, consisting of the essential pollen-cell and a layer of secretion (the external pollen membrane). It has four circular clefts, in which the pollen lies free (uncovered).

*Fig.* 18. Section of the pollen-membrane. *c*, Essential membrane of the pollen-cell; *b*, layer of secretion; *d*, projections formed of the same substance, and in union with the layer of secretion. It forms the reticulated united elevations on the whole surface of the granule. The little pits or cavities thus formed are filled with a clear, firm, gelatinous substance, *a*, perhaps the residuum of the dissolved parent-cells.

What I have observed on the development of the pollen, I have here, and in the text on other plants, communicated. Whether myself or Nägeli is right, or both wrong, the future alone can decide.

## Plate V.

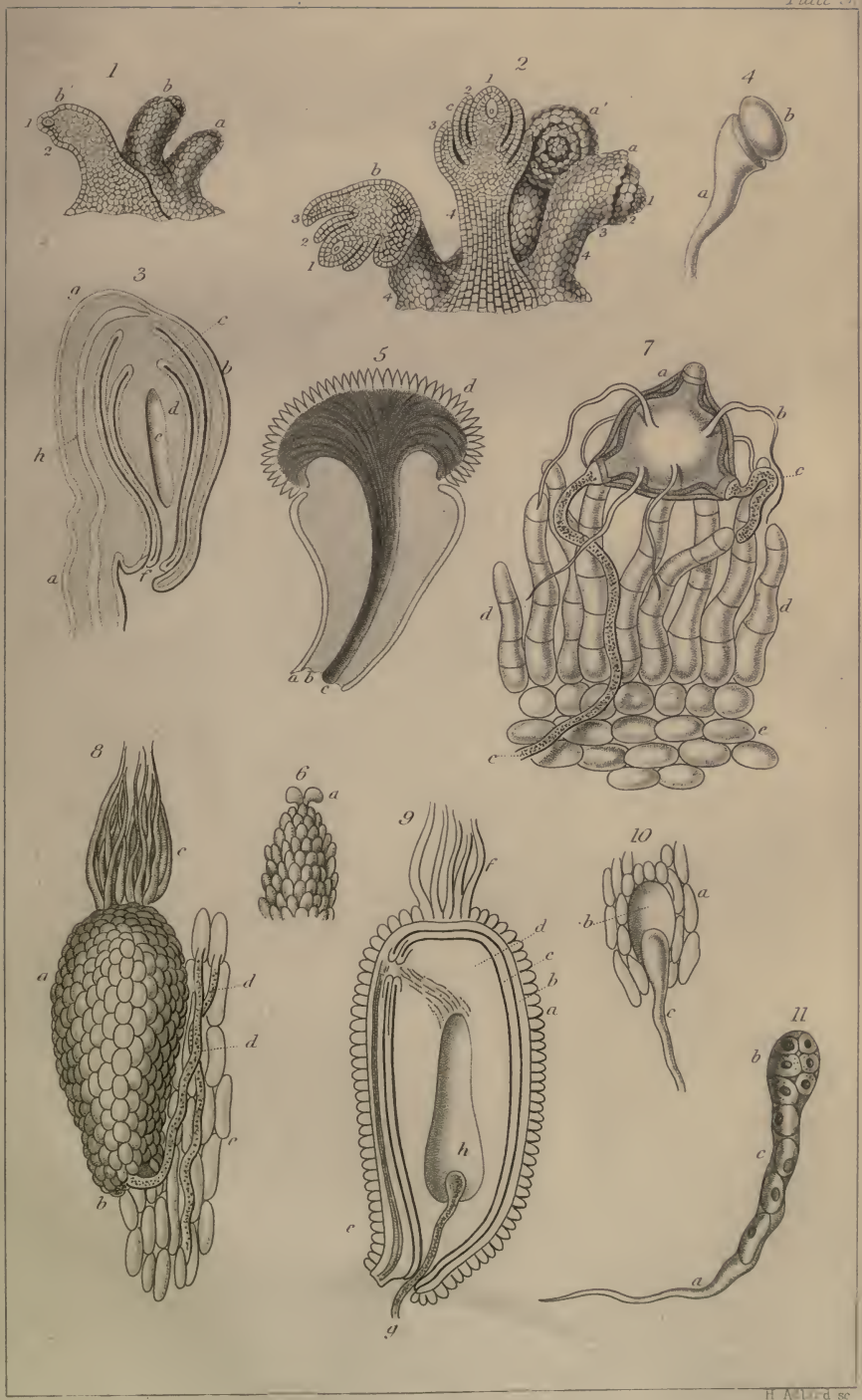
### *Development of the Seed-bud* (Ovule), *Stigma, and Embryo.*

Figs. 1—3. Development of the Seed-bud in *Passiflora princeps.*

*Fig.* 1. Three seed-buds at a period somewhat earlier than fig. 11. *a*, Very young seed-bud, forming a simple, rather curved wart (the nucleus of the bud and the stalk of the bud undistinguishable); *b*, a seed-bud further developed, in which the first integument is already formed, and which embraces the base of the nucleus so as to distinguish it from the peduncle of the bud (*funiculus*); *b′*, longitudinal section of one in a medium condition; 1, point of the nucleus (nuclear wart); 2, appearance of the first integument. At the point of the nucleus is seen a strikingly-enlarged cell containing cytoblasts: this is the future embryo-sac.

*Fig.* 2. Seed-bud at a somewhat later period than fig. 11. (Pl. IV.) *a*, The nucleus already covered with the first integument, 2, and this again with a second, 3, so that the peduncle (4) of the bud is perfectly separated; *a′*, a similar bud seen in front; *b*, longitudinal section of the upper part of a somewhat further developed bud, which is explained fig. 1 *b′* and fig. 2 *a*; *c*, a seed-bud unfolding in an abnormal way. The figures are the same as in *a*. The contrast is striking in this case between the cells of the peduncle (4) of the bud, arranged in long rows, and, on account of the air in the intercellular passages, of a black colour, and the round, succulent, cellular tissue of the seed-bud.

*Fig.* 3. Longitudinal section of a perfectly-developed (inverted) seed-bud before impregnation. *a*, Peduncle of the bud; *b*, external integument; *c*, internal integument; *d*, nucleus, *e*, embryo-sac; *f*, opening of the bud (micropyle); *g*, base of the bud; *h*, raphe.

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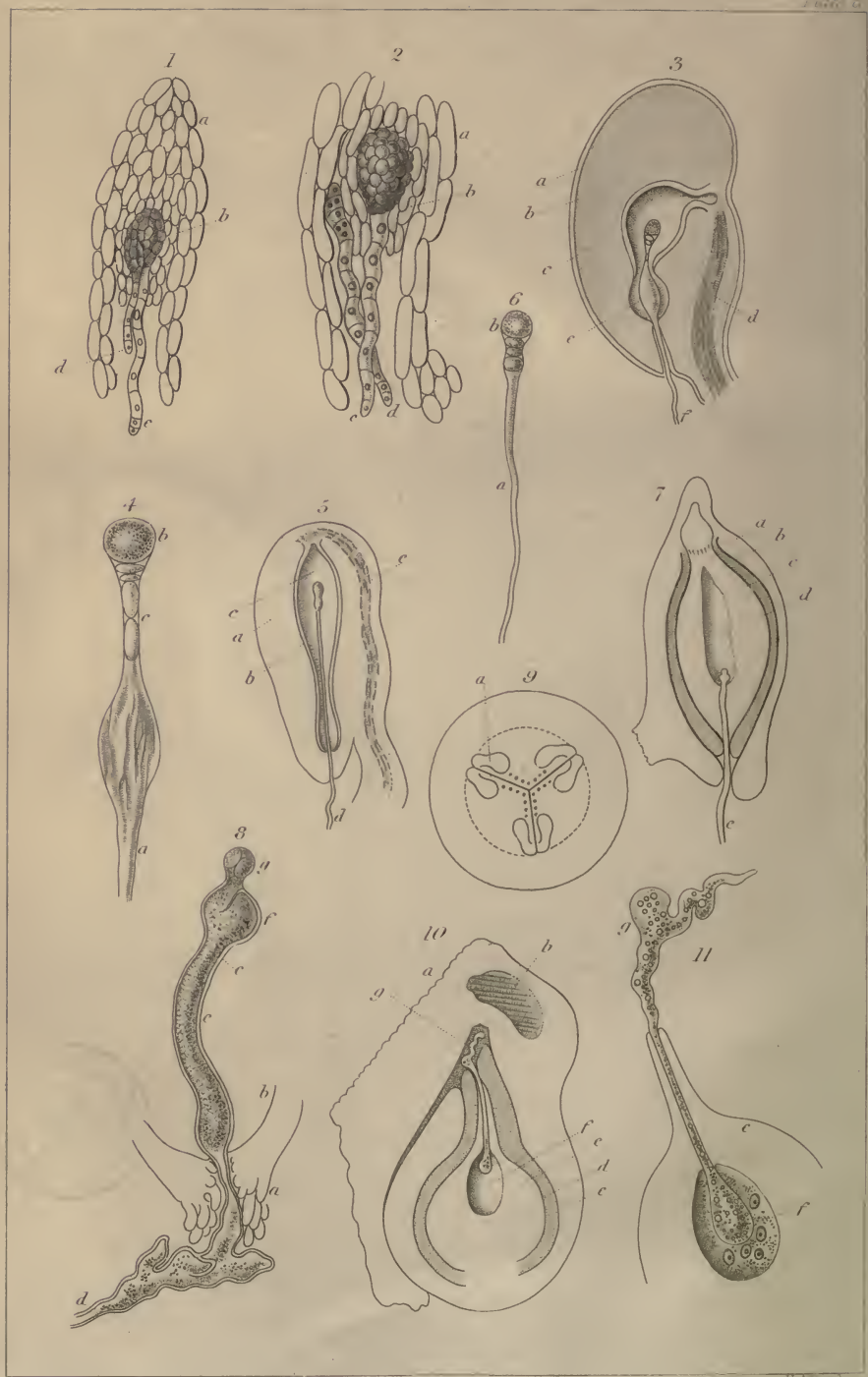


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Figs. 4—6. Formation of the Stigma.

*Fig.* 4. *a*, Style ; *b*, stigma, slightly magnified.

*Fig.* 5. Longitudinal section of part of the style and stigma. *a*, Epidermis ; *b*, parenchyma ; *c*, canal of the style, in which is continued the delicate gelatinous parenchyma of the stigma as a conducting cellular tissue ; *d*, papilla of the stigma.

*Fig.* 6. An individual stigmatic papilla, strongly magnified, terminating in two papillary cells (*a*), between which eventually the pollen-tube penetrates.

## Development of the Embryo.

Figs. 7—9. *Epilobium hirsutum.*

*Fig.* 7. A small portion of the stigma. *a*, Pollen-grain with detached fibres (*b*) and two pollen tubes (*c*), of which the left has already penetrated through the papillæ (*d*) to the parenchyma (*e*) of the stigma.

*Fig.* 8. *a*, The seed-bud and a portion of the conducting cellular tissue (*e*) of the germen. The pollen-tubes (*d d*) are passing down the conducting cellular tissue, and one of them enters the foramen (*b*) of the seed-bud (ovule); *c*, hairs of the seed-bud at its base.

*Fig.* 9. Longitudinal section through the foregoing seed-bud. *a*, Papillary epidermis ; *b*, parenchyma of the external envelopes of the bud ; *c*, internal envelope ; *d*, nucleus ; *e*, raphe ; *f*, tuft of hair at the base of the seed-bud ; *g*, pollen-tube entering the foramen ; *h*, sac of the embryo.

Figs. 10. and 11. *Orchis Morio.*

*Fig.* 10. Soon after the entrance of the pollen-tube. *a*, Inner integument : *b*, sac of the embryo, which has perfectly supplanted the nucleus ; *c*, pollen-tube.

*Fig.* 11. Prepared free from the seed-bud. *a*, The pollen-tube, which clearly as a continuous membrane surrounds the cells which are contained in it, and of which (*b*) forms the embryo ; *c*, the peduncle of the embryo (embryoträger), which at a later period projects from the seed-bud.

## Plate VI.

### Development of the Embryo—*continued.*

Figs. 1. and 2. *Orchis latifolia.*

*Fig.* 1. Longitudinal section of a seed-bud. *a*, External integument ; *b*, internal integument ; *c*, *d*, two pollen-tubes, whose penetrating extremities have formed the foundation of two embryos.

*Fig.* 2. Longitudinal section of the lower part of a seed-bud. *a—d*, As in fig. 1. The pollen-tube, *c*, has penetrated the right spot and has developed a perfect embryo ; but the other, *d*, has missed the inner foramen and passed between the internal and external integument, and in this case has formed a rudimentary embryo.

Figs. 3. and 4. *Salvia bicolor.*

*Fig.* 3. Longitudinal section through the seed-bud. *a*, Epidermis of the simple integument (*b*) ; *c*, the epidermis of the supplanted nucleus (*membrana nuclei*, Rob. Brown) ; *d*, raphe ; *e*, the sac of the embryo, which has extended itself above the nucleus into the canal of the foramen of the seed-bud ; *f*, pollen-tube penetrating into the embryo-sac, where it lays the foundations of the embryo.

*Fig.* 4. Pollen-tube prepared from the foregoing. *a*, The under, looser part dilated (with the extension of the embryo-sac) ; *c*, upper portion attenuated and filled with some cells which subsequently form the peduncle of the embryo ; *b*, large globular cell developed at the extremity of the pollen-tube, and which is the basis of the embryo.

Figs. 5. and 6. *Martynia diandra.*

*Fig.* 5. Longitudinal section through the seed-bud. *a*, Simple integument; *b*, the remaining epidermis of the nucleus; *c*, the sac of the embryo already filled with a delicate endosperm; *d*, the pollen-tube which runs almost through the whole length of the embryo-sac to the base of the seed-bud; *e*, raphe.

*Fig.* 6. Pollen-tube prepared from the foregoing: *b*, a large globular cell which forms the foundation of the future embryo; lying under this cell are some others, which form the peduncle of the embryo.

Figs. 7. and 8. *Œnothera rhizocarpa.*

*Fig.* 7. Longitudinal section through the seed-bud. *a*, External; *b*, internal integument; *c*, nucleus; *d*, sac of the embryo; *e*, pollen-tube.

*Fig.* 8. Pollen-tube separated from the foregoing. *a*, Internal integument; *b*, nucleus; *c*, sac of the embryo; *d*, pollen-tube, which in passing through the internal and external integument exhibits irregular bulgings and contractions, in order to pass through the inner foramen of the seed-bud. It then again becomes broader (*e*) as it passes through the nucleus, and at *f* presents a considerable enlargement (which subsequently becomes the peduncle (*g*) of the embryo); it then again contracts, and at last terminates in a little vesicle which eventually becomes the embryo. As the pollen-tube contains in its sap a good deal of albumen, it becomes coloured of a dark yellow colour, and almost opaque, when treated with tincture of iodine.

Figs. 9—11. *Momordica Elaterium.*

*Fig.* 9. Transverse section of the germen. *a*, The seed-buds, which are represented in the following figure: —

*Fig.* 10. Longitudinal section through a seed-bud and a part of the spermophore; *a*, conducting cellular tissue; *b*, peculiar group of spiral vessels in the spermophore; *c*, external; *d*, internal integument; *e*, nucleus; *f*, sac of the embryo; *g*, pollen-tube.

*Fig.* 11. Point of the nucleus prepared from the foregoing: *e*—*g*, as in the previous figure. In the embryo-sac are visible cell-nuclei and young cells, the commencement of an endosperm. The pollen-tube, before its entrance into the seed-bud, forms a considerable irregular enlargement; it then passes through the elongated nipple of the nucleus, and forms a very considerable vesicular enlargement in the embryo-sac, which is the foundation of the future embryo.

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